





the genus. These included the presence of alate palea keels, nondistichous inflorescences, three-parted styles, sterile lower florets, and a well-defined geographical distribution. However, these morphological characteristics are not completely consistent because they are known to appear in species from both hemispheres. This led Hackel (1887) to include *Guadua* as a subgenus of *Bambusa*. Munro's (1868) monograph was influential in the acceptance of *Guadua* as a genus, even though he expressed doubts as to its validity. After 1868, the group was generally treated as *Guadua* until McClure (1973), uncertain of its generic separation, reduced it to a subgenus of *Bambusa*.

In their study of the genera of American bamboos with pseudospikelets, Soderstrom & Londoño (1987) restored *Guadua* to generic status based on a number of distinctive features, i.e., a triangular culm leaf in which the margins of the sheath and blade are contiguous or almost so, presence of thorns on the culms and branches, a distinctive band of short white hairs both above and below the nodal line, and a palea of firm texture with prominent wings emanating from the keels.

We are following this most recent treatment of the group and use the name *Guadua*. Monographic studies of the genus and related groups will be needed to further clarify generic limits.

#### *GUADUA ANGUSTIFOLIA* KUNTH

Humboldt & Bonpland (1806) described *Bambusa guadua* and *B. latifolia* based on specimens made during their 1799–1804 South American voyage. These were the first of the more than 30 species of New World bamboos of the genus *Guadua* to be described. In addition to Latin and French descriptions, illustrations and observations on local uses and ecology were provided for both species. The specific epithet *guadua* came from the common name used by the people of Colombia. This name is still in use and is usually pronounced guá-du-a in Colombia and gua-dú-a in Ecuador. Poiret (1808), using Humboldt's information, also published an extensive description of *B. guadua* and discussed its economic uses.

When Kunth (1822a) transferred *Bambusa guadua* and *B. latifolia* to his new genus *Guadua*, he failed to specify which species was to be the type. McClure later selected *B. guadua* as the type, citing, "The internal evidence as to which species he [Kunth] probably had principally in mind consists of the extensive documentation by Humboldt and Bonpland (l.c. 63 et seq) of *B. guadua* (basis of *Guadua angustifolia*) in relation

to the local economy and to the flora of the type locality" (McClure, 1957: 203). Kunth avoided the use of a tautonym by changing *B. guadua* to *G. angustifolia*, referring to the narrow branch leaves that distinguish it from *G. latifolia*. This narrow-leaved characteristic has subsequently been found in many species of the subgenus, and its use as a diagnostic feature is limited. *Guadua angustifolia* is the name most often found in the literature and has been used in recent years (Burkart, 1969; Rosengurtt et al., 1970; Purseglove, 1972; Azevedo Correa et al., 1977; Azzini et al., 1977a, b; Soderstrom & Londoño, 1987), although *B. guadua* has frequently appeared (Hidalgo López, 1974; Turpe, 1975; Rincón Sepúlveda, 1977; Hidalgo López, 1978; Smith et al., 1981; Maecha Vega & Echeverri Restrepo, 1983; Soderholm, 1984).

#### *GUADUA ACULEATA* RUPR. EX FOURN.

Ruprecht first used the name *Bambusa aculeata* (meaning thorny) after examining and annotating specimens from the 1841–1842 Mexican journey of the little-known German collector Wilhelm von Karwin (Karwinsky). Fournier (1877), after seeing Karwinsky's specimens, used the name *Guadua aculeata* in a discussion of polygamy in pseudospikelets, but no formal description appeared until the publication of Fournier's *Mexicanas Plantas* (1886). Seven specimens were listed as syntypes, five from Colipa, Veracruz, and two from unknown Mexican localities.

Fournier also described another of Ruprecht's "herbarium species" with the name *Guadua intermedia*. The name probably referred to the position of the branch leaves, which are intermingled with the spikelets. Leaves are also in this position in *G. aculeata* and *G. angustifolia*. The only difference between the original descriptions of *G. intermedia* and *G. aculeata* is the length of the spikelets, described as short in *G. aculeata* and more than 5.1 cm long in *G. intermedia*. The few spikelets seen from the type collection are about 2.5 cm long and are indistinguishable from those of *G. aculeata*. *Guadua intermedia* appears two more times in the literature without further elaboration of Fournier's description (Hemsley, 1885; Camus, 1913). McClure (1973) included it as a synonym of *B. aculeata*.

Another species that McClure synonymized under *Bambusa aculeata* is *Guadua inermis* (meaning thornless), which he was not able to distinguish from *B. aculeata* on the basis of inflorescences in their respective type collections (McClure, 1973). The only differences between these presumed spe-



cies, upon reading the original descriptions, are their thorniness and spikelet size (i.e., *B. aculeata* with seven florets per spikelet and thorns, and *G. inermis* with eight to nine florets per spikelet and thornless). A thornless form of the similar species, *G. amplexifolia* Presl, also occurs sympatrically with *G. aculeata* in southern Mexico and further confuses assessment of taxonomic affinities of *G. inermis*. (This problem is discussed in more detail under interspecific relationships.) Unfortunately, culm leaves were neither collected, illustrated, nor described for these species when they were first collected and thus cannot be used to clarify the taxonomic disposition of these names. Hitchcock (1913) transferred *G. aculeata* to *Bambusa* and included it in his listing of the Mexican grasses in the U.S. National Herbarium. He mistakenly gave credit to Ruprecht for describing the species, an error that was carried over to McClure's (1973) work. The correct citation in the genus *Bambusa* is *B. aculeata* (Rupr. ex Fourn.) Hitchcock.

#### BAMBUSA CHACOENSIS N. ROJAS

The large bamboos of the subtropical regions of Argentina and Paraguay have rarely been described in the literature. Nicolas Rojas Acosta, an Argentine botanist known for his unorthodox methods and fragmentary descriptions, described these bamboos under the name *Bambusa chacoensis* (Rojas Acosta, 1918). His description was so vague as to encompass many of the species now included in the genus, but his locality data and the common name he used, "tacuara," distinguish it from the other bamboos that grow in its range (i.e., *Guadua paraguayana* Doell ex Mart. and *G. paniculata* Munro, "la picanilla"; and *G. trinii* (Nees) Rupr. and *G. tagoara* (Nees) Kunth, "tacuarazú"). Unfortunately, he regarded nature itself as his herbarium and generally did not collect specimens (Krapovickas, 1970). Consequently, he did not collect a specimen of this bamboo nor did he designate a type specimen.

In 1931 this species appeared in a key as *Bambusa guadua* (Anonymous, 1931). The similarity of these bamboos to *Guadua angustifolia* led Parodi (1936) to identify them as *G. angustifolia*. Whether Parodi knew of Rojas Acosta's description and disregarded its validity is not known, but in all subsequent literature these bamboos have been identified as *G. angustifolia* (Lombardo, 1943; Parodi, 1943; Ragonese, 1943; Young, 1946; Burkart, 1969; Rosengurtt et al., 1970) or *B. guadua* (Roseveare, 1948; Turpe, 1975). McClure (1973) included *B. chacoensis* as an unre-

solved specific taxon, and only recently Quarín (1977), Soderstrom (1981), Nicora & Rúgolo de Agrasar (1987) and Londoño & Peterson (1992) chose to resurrect the name *B. chacoensis*. Only two published photographs, both long-distance views, are known to exist of *B. chacoensis* (Short, 1975).

#### PAST COMPARISONS

These three groups of bamboos have never been satisfactorily separated in a key or adequately compared. *Guadua angustifolia* has been separated from *G. aculeata* only once, by Camus (1913), but the distinction was based on the presence (*G. aculeata*) or absence (*G. angustifolia*) of thorns. It is now known that these two bamboos show various degrees of thorn development.

McClure (1955) included detailed descriptions of *Guadua aculeata* and *G. angustifolia* in the *Flora of Guatemala*, but failed to separate the two in the same key. He included two forms of *G. angustifolia* in a separate key to introduced bamboos, but none of the characteristics coincided with those included in the key to native species containing *G. aculeata*.

*Bambusa chacoensis* has rarely been considered different from *Guadua angustifolia*, and therefore has never been separated from it in a key. Rojas Acosta did not seem to be aware of *G. angustifolia* and made no attempt to compare *B. chacoensis* with this species. Londoño & Peterson (1992) compare *G. angustifolia*, *G. trinii* and *G. chacoensis* in a table and conclude that *G. chacoensis* is a separate species more closely related to *G. trinii* than *G. angustifolia*. However, they do not include information from the entire range of *G. angustifolia* and exclude important characters such as size ratio of culm leaf blade to the entire culm leaf.

#### MATERIALS AND METHODS

This investigation involved field studies, traditional taxonomic methods utilizing herbarium specimens, and multivariate statistical analyses of the *Guadua angustifolia* complex.

#### HERBARIUM STUDIES

A Wild dissecting microscope was used to examine 105 herbarium specimens for vegetative features and 51 specimens for reproductive features. Measurements were taken with an ocular micrometer and calibrated using a stage microm-



TABLE 1. Foliage leaf characters used in principal components analysis. \* = omitted from analysis of culm and foliage leaf data.

1. Leaves per complement
2. Position on sheath of hairs sized $\geq 0.1$ mm
3. Position on sheath of hairs sized $\leq 0.09$ mm*
4. Density on sheath of hairs sized $\geq 0.1$ mm
5. Degree of stramineous coloration in sheath
6. Degree of brown coloration in sheath
7. Degree of purple coloration in sheath*
8. Degree of green coloration in sheath
9. Number of oral setae
10. Length of oral setae
11. Degree of stramineous coloration in oral setae
12. Degree of white coloration in oral setae
13. Degree of brown coloration in oral setae
14. Degree of purple coloration in oral setae
15. Sheath auricle length
16. Leaf auricle width
17. Collar length
18. Collar flaring
19. Ligule height
20. Position on ligule of hairs sized $\leq 0.09$ mm*
21. Position on ligule of hairs sized $\geq 0.1$ mm
22. Pulvinus height
23. Degree of stramineous coloration on pulvinus
24. Degree of brown coloration on pulvinus
25. Degree of green coloration on pulvinus*
26. Degree of purple coloration on pulvinus*
27. Pulvinus vesture
28. Position on adaxial petiole of hairs sized $\leq 0.09$ mm
29. Position on adaxial petiole of hairs sized $\geq 0.1$ mm
30. Density of adaxial petiole hairs sized $\leq 0.09$ mm
31. Density of adaxial petiole hairs sized $\geq 0.1$ mm
32. Position on abaxial petiole of hairs sized $\leq 0.09$ mm
33. Position on abaxial petiole of hairs sized $\geq 0.1$ mm*
34. Density of abaxial petiole hairs sized $\leq 0.09$ mm
35. Density of abaxial petiole hairs sized $\geq 0.1$ mm*
36. Blade width
37. Blade length
38. Blade width to length ratio*
39. Blade adaxial hair distribution
40. Blade adaxial hair density
41. Blade abaxial hair distribution
42. Blade abaxial hair density

eter. Each specimen usually consisted of several sheets.

#### NUMERICAL TECHNIQUES

The fragmentary and incomplete nature of bamboo herbarium specimens prevented the simultaneous gathering of detailed vegetative and reproductive data from all but a few herbarium specimens. In order to include as many specimens as possible, data (consisting of continuously varying or "count"

TABLE 2. Foliage and culm leaf characters included in second PCA with foliage leaf characters.

1. Thorn development
2. Culm leaf sheath length
3. Culm leaf sheath base width
4. Culm leaf sheath ligule width
5. Culm leaf blade length
6. Culm leaf blade to culm leaf ratio
7. Culm leaf sheath vesture
8. Culm leaf blade vesture
9. Contact of ligule with culm leaf margin
10. Density of culm leaf ligule cilia
11. Length of culm leaf ligule cilia

characters) are analyzed in four separate categories, two vegetative and two reproductive.

The first vegetative data set includes 42 characters measured from the foliage leaves of 105 specimens. These characters are listed in Table 1. The second vegetative data set includes selected branch leaf data plus 11 additional characters from culm leaves and branches of 65 specimens. These additional characters are listed in Table 2. Another 24 vegetative characters were measured but omitted from the analyses because of inadequate herbarium material, distortion in pressed material, or their extreme variability.

The first reproductive data set includes 33 characters measured by examining the external features of inflorescences and spikelets of 49 specimens. These characters are listed in Table 3. The second reproductive category includes all external features plus seven internal characters from dissected spikelets of 30 specimens. These additional characters are listed in Table 4. Another 33 characters were measured and omitted from the analyses because they proved to be too variable.

A total of 152 vegetative and reproductive characters were measured during the course of study. The absence of any previous detailed studies of this group necessitated the use of a large number of characters in order to understand adequately the pattern of variation of the group.

The data were analyzed by Principal Components Analysis (PCA) using the program CLUSTAN (Wishart, 1975); see discussion of this ordination technique in Wiley (1981). Results are presented in the taxonomic treatment section of this paper.

#### SPECIES CONCEPT

In the Bambusoideae the challenge of delimiting and ranking taxa is complicated by the absence of complete herbarium specimens. A reproductive system that produces flowers only after many years



TABLE 3. External reproductive characters used in principal components analysis.

1. Number of lateral leaves in inflorescence
2. Number of terminal leaves in inflorescence
3. Spikelets per cluster
4. Spikelet length
5. Spikelet width
6. Spikelet stature (erect to arcuate)
7. Number of gemmiparous bracts
8. Uppermost gemmiparous bract length
9. Uppermost gemmiparous bract width
10. Degree of stramineous coloration in bract
11. Degree of brown coloration in bract
12. Degree of purple coloration in bract
13. Degree of green coloration in bract
14. Number of veins on bract
15. Density of hairs at base of bract
16. Density of hairs at center of bract
17. Density of hairs at apex of bract
18. Density of hairs on edges of bract
19. Number of florets
20. Lowermost lemma length
21. Lowermost lemma width
22. Lowermost lemma mucro length
23. Degree of stramineous coloration on lemma
24. Degree of brown coloration on lemma
25. Degree of purple coloration on lemma
26. Degree of green coloration on lemma
27. Number of veins on lemma
28. Density of short hairs at base of lemma
29. Density of short hairs at center of lemma
30. Density of short hairs at apex of lemma
31. Density of short hairs on edges of lemma
32. Density of long hairs at base of lemma
33. Density of long hairs at center of lemma

of vegetative growth drastically reduces the opportunity to observe, collect, and experiment with reproductive structures, a situation McClure (1973) likened to the system of "Fungi Imperfecti" developed by mycologists. These problems have limited our knowledge of the processes involved in bamboo speciation and have kept bamboo taxonomy from advancing much beyond the alpha stage.

Past bamboo classifications have been based strictly upon overall similarity and the presence of gaps in observed morphological patterns rather than hypothesized evolutionary changes or biological interactions. While this system is not ideal, constraints of time and the problems referred to above have limited the present study to a similar approach.

Species will be delimited here on the basis of consistent morphological gaps in a number of vegetative and/or reproductive characters. The category of subspecies will be considered synonymous

TABLE 4. Interior spikelet characters used in principal components analysis.

1. Lowest rachilla section length
2. Lowest rachilla section width
3. Lowermost palea length
4. Lowermost palea width between keels
5. Style length
6. Style width
7. Style hair length

with that of variety as proposed by Raven (1974). Both categories have been used sparingly by bamboo taxonomists (Munro, 1868; Camus, 1913; Holttum, 1958; McClure, 1973), but in this study subspecies will be used to delimit populations that are geographically isolated and exhibit variation, which results in slight morphological gaps of a few vegetative and/or reproductive characters. Populations that vary in a few vegetative and/or reproductive characters and show some geographic continuity but no consistent morphological gaps are referred to as "incipient geographic races."

#### INTERSPECIFIC RELATIONSHIPS AND DEFINITION OF THE *GUADUA ANGUSTIFOLIA* COMPLEX

The genus *Guadua* is in need of revision, since many of the species have been inadequately described and collected. However, the species of the *G. angustifolia* complex are clearly separable from the remaining taxa. The combination of characters that define the *G. angustifolia* complex are as follows: culms of large stature (i.e., (7-)10-20(-30) m tall), erect with arched tops; internode walls of medium thickness; culm leaves large, abaxially pubescent, and usually without auricles; foliage leaf sheath glabrous or pubescent toward midrib of lower half, sometimes approaching the apex but never present there; foliage leaf blade about 10-25 cm long and 1-4 cm wide, surfaces glabrous or only sparsely pubescent, petioles glabrous along midrib of abaxial surface. Synflorescence consisting of 2-5 multiflowered pseudospikelets on delicate, branching twigs; main florescence 2-9 cm long and 3-8 mm wide; florets 3-14; surface of bracts and lemmas glabrous or with sparse hyaline hairs at base, center, and edges, rarely densely pubescent at base and center, margins glabrous; palea keels with pubescent margins exerted beyond the lemmas; lodicules 3.

Most plants in the genus do not grow taller than 10 m, while plants of *Guadua angustifolia* usually grow to between 10 and 20 m and are often taller, sometimes reaching 30 m. The other large species



of the genus are few and are easily separated from *G. angustifolia* by several vegetative and reproductive characters. In Tables 5 and 6, a detailed comparison is made among the species that are sympatric with *Guadua angustifolia*.

Although the species sympatric with *Guadua angustifolia* are easily separated from this species on vegetative and floral characters, the scarcity of *G. angustifolia* subsp. *angustifolia* in Mexico and Central America (formerly known as *G. aculeata*) has caused problems in the past. Two forms of *G. amplexifolia* are more common than *G. angustifolia* in Mexico and Central America. As a result, *G. amplexifolia* has often been misidentified as *G. aculeata*. This problem developed because of the lack of detailed vegetative descriptions and a vegetative key separating the two species. Both *G. amplexifolia* and *G. angustifolia* are very thorny, and early collections were given the name *G. aculeata*. Once these collections were misidentified the error was carried over to the determinations of later specimens. Another problem concerns the thornless forms of *G. amplexifolia* and *G. angustifolia*. The thornless form of *G. angustifolia* in Mexico, originally named *G. inermis*, was described from flowering material from Colipa, Veracruz. The culms were described as 16 m tall and unarmed, and the branch leaf sheaths and petioles were described as glabrous, all characteristics of *G. angustifolia*. There are some clumps of *G. angustifolia* in other parts of its range (mainly in the province of Esmeraldas, Ecuador) that have few or no thorns on the upper branches. When branches on the lower third of the culm, which are thorny, fail to develop, the culm could be considered thornless. *Guadua inermis* likely has this same growth form. Unfortunately, there is no complete vegetative specimen of *G. inermis* from Mexico and, because its occurrence is so restricted, no living plants may remain.

The thornless form of *Guadua amplexifolia*, which occurs in many areas of Central America, has not been described in the literature and thus has often been misidentified as *G. inermis*. It is readily distinguishable from *G. angustifolia* on the basis of size, culm spacing, wall thickness, culm leaves, and foliage leaves (see Table 5). These plants (which have been collected in Mexico by the first author) can be separated from the thorny and solid-culm form of *G. amplexifolia* by their hollow but thick-walled culms. Thus, we have chosen to call this form "hollow culm." While "hollow culm" almost always lacks thorns, they may be present in reduced numbers. More study is needed to de-

termine the precise taxonomic relationship of the "hollow culm" form to typical *G. amplexifolia*.

#### PHYTOGEOGRAPHY

*Guadua angustifolia* has the widest geographic range of any species in *Guadua*. Its northernmost localities are found in the state of Veracruz, Mexico, and its southernmost localities are found in northeastern Argentina and southeastern Paraguay. *Guadua angustifolia* is one of only three species that are known from both Central and South America; the others are *G. paniculata* and *G. amplexifolia*.

Speculation on the factors resulting in such extensive distributions is difficult because of the paucity of information on the mechanisms of dispersal of these large bamboos. Discontinuities in flowering periods can be very long, up to 35 years, and no studies have been made to ascertain the vectors responsible for seed dispersal or seed-dispersal distances of these bamboos. Vegetative dispersal must certainly be a factor in increasing their range; studies have been done that show the ease with which culms root when planted (McClure, 1966). These large bamboos frequently grow along riverbanks, and floods could serve as an efficient means of vegetative dispersal, especially downstream.

Long-distance dispersal between continents or islands could possibly occur when culm sections are carried by ocean currents. No studies have tested the viability of culms after prolonged exposure to seawater, but the first author has observed clumps growing within a kilometer of the ocean and on islands within tidal bays. Raven & Axelrod (1974) suggested that bamboos found north of Panama probably arrived in Neogene times or even more recently from South America. It is interesting that only three species of *Guadua* have a bicontinental distribution, and even more intriguing is the fact that no large bamboos are native to the islands of the West Indies (except Trinidad, which is geologically part of South America). This suggests that oceanic transport is not a common means of dispersal.

Even though *Guadua angustifolia* is found from Mexico to Argentina, there are large gaps in its distribution (Figs. 2-4). Throughout Central America it is not very common and, as McClure (1955) suggested, it may have been extirpated from much of its former range by selective cutting of its superior culms. In his personal notes he wrote, "According to the late Dr. Ross E. Moore, who spoke from personal experience covering many years as



TABLE 5. A morphological comparison of *Guadua angustifolia* subsp. *angustifolia* and other sympatric species of *Guadua*.

	<i>Guadua angustifolia</i> subsp. <i>angustifolia</i>	<i>Guadua amplexifolia</i> "solid culm"	<i>Guadua amplexifolia</i> "hollow culm"	<i>Guadua longifolia</i>	<i>Guadua paniculata</i>
Culms	erect; 10–30 m tall, 10–20 m diam.; medium wall thickness	erect; 8–10 m tall, 6–10 cm diam.; solid with pithy center	erect; 8–10 m tall, 6–10 cm diam.; thick-walled	clambering; to 15 m long, to 5 cm diam.; thick-walled	weakly erect; 8–9 m tall, 5–7 cm diam.; thick-walled
Culm leaves	brown pubescent; deciduous; blade about $\frac{1}{4}$ or less as long as leaf, persistent; auricles absent	brown pubescent; tardily deciduous to persistent and rotting; blade $\frac{1}{3}$ to $\frac{1}{2}$ as long as leaf, persistent; auricles present to absent	brown pubescent; tardily deciduous to persistent and rotting; blade $\frac{1}{3}$ to $\frac{1}{2}$ as long as leaf, persistent; large auricles present	slightly white pubescent; promptly deciduous; blade about $\frac{1}{3}$ as long as leaf, base much lower on one side; auricles absent	yellow-green with purple horizontal stripes, pubescent; sheath tardily deciduous; blade $\frac{1}{2}$ to $\frac{1}{3}$ as long as leaf, caducous from sheath; auricles absent
Thorns	present to rarely absent; 1–5 at the node; short to long	present; 1–5 at node; short to long	absent to very sparse; few at node if present; short	present; 1 or rarely 2 at node, pointing downward	present; usually 3 at node; fairly long, slender and very sharp
Branch leaves	blades medium width; sheaths glabrous or pubescent along midrib of lower half; abaxial petiole glabrous; auricles absent to rarely present	blades medium to wide; sheaths glabrous to totally pubescent, usually on edges of lower or upper half; abaxial petiole glabrous; auricles absent to present	blades wide; sheaths usually glabrous; abaxial petiole glabrous; auricles present	blades very narrow; sheaths glabrous to rarely pubescent; abaxial petiole glabrous to pubescent; auricles present to absent	blades narrow, pendant; sheaths pubescent; abaxial petiole pubescent; auricles absent
Spikelets	short to long, narrow, flattened; 1–3 per cluster; glabrous to slightly pubescent	long and wide, rarely short, round; usually 3 or more per cluster; glabrous to rarely pubescent	same as "solid culm"	very long and narrow, round; 1–3 per cluster; glabrous	short and narrow, flattened; usually 3 or more per cluster; pubescent



TABLE 6. A morphological comparison of *Guadua angustifolia* subsp. *chacoensis* and other sympatric species of *Guadua*.

	<i>Guadua angustifolia</i> subsp. <i>chacoensis</i>	<i>Guadua paraguayana</i>	<i>Guadua trinii</i>	<i>Guadua tagoara</i>	<i>Guadua paniculata</i>
Culms	10–15 m tall, 8–10 cm diam.	8–10 m tall, 2–4 cm diam.	8–10 m tall, 3–5 cm diam.	8–10 m tall, 6–8 cm diam.	8–9 m tall, 5–7 cm diam.
Culm leaves	brown pubescent; blade $\frac{1}{4}$ or less as long as leaf, persistent; auricles absent	brown pubescent; blade $\frac{1}{3}$ as long as leaf, persistent; auricles present	brown pubescent; blade $\frac{1}{2}$ as long as leaf, persistent; auricles absent	brown pubescent; blades $\frac{1}{6}$ as long as leaf, much wider than long, persistent; auricles absent	yellow-green with purple horizontal stripes, pubescent; blade $\frac{1}{2}$ to $\frac{1}{3}$ as long as leaf, caducous from sheath; auricles absent
Branch leaves	blades medium to narrow; sheaths glabrous; abaxial petiole glabrous	blades medium to narrow; sheath with hairs on one or both sides of apex; abaxial petiole pubescent on one or both sides	blades medium to narrow; sheaths glabrous to pubescent at apex; abaxial petiole glabrous to pubescent	blades wide; sheaths pubescent on one side of apex; abaxial petiole glabrous	blades narrow, pendant; sheaths pubescent; abaxial petiole pubescent
Spikelets	long and wide, glabrous to slightly scabrous; palea wings exserted, ciliate	long to short and narrow, pubescent; palea wings usually not exserted, ciliate	short and narrow, glabrous; palea wings broadly exserted, glabrous to minutely ciliate	short and narrow, glabrous; palea wings broadly exserted, not ciliate	short and narrow, pubescent; palea wings not exserted, ciliate



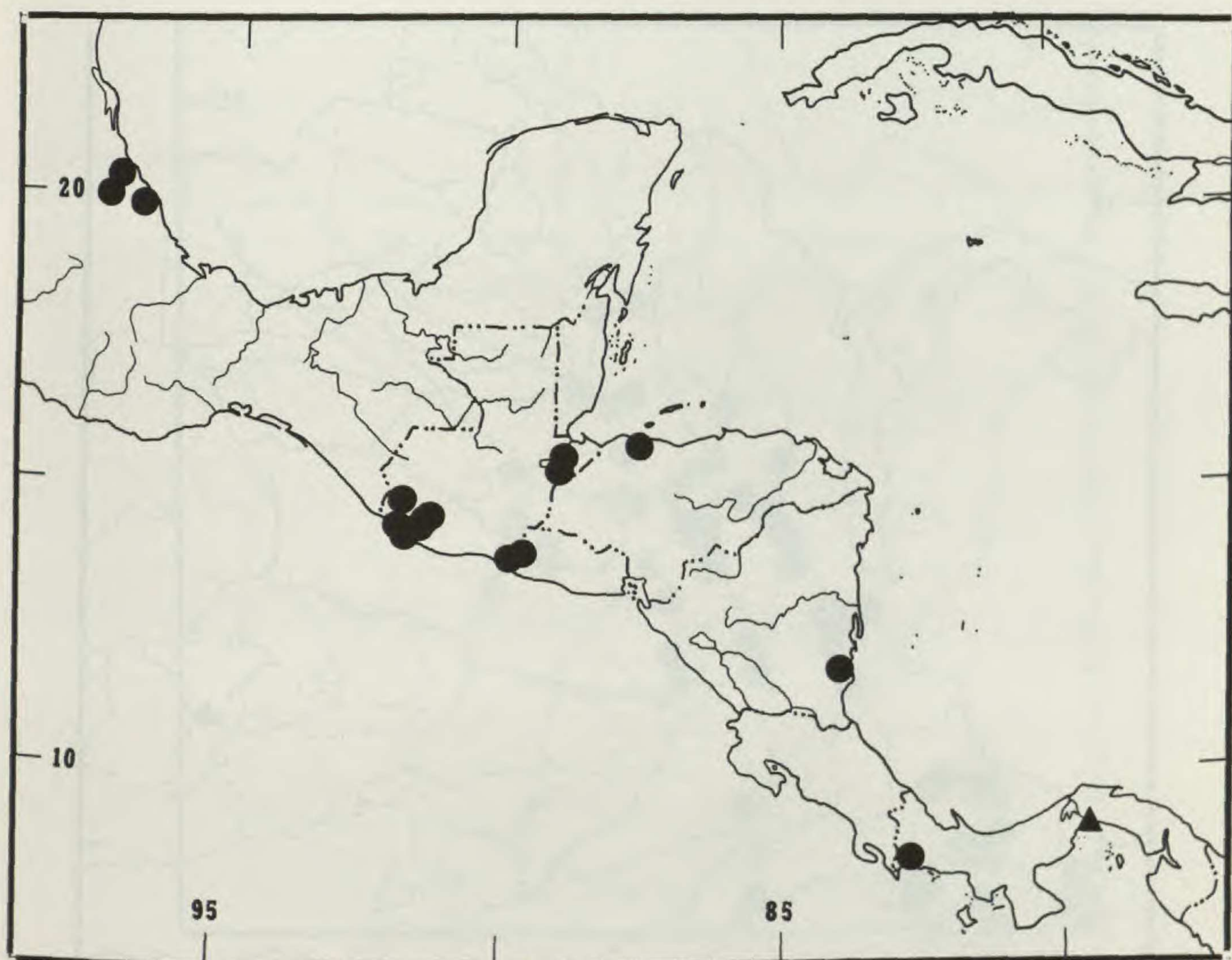


FIGURE 2. Distribution of the northern populations of *Guadua angustifolia* subsp. *angustifolia*. Dots = native plants; triangle = possible cultivated plant.

a consultant on land utilization in several countries of Central America, thousands of acres of land originally occupied by more or less pure stands of bamboo [*G. amplexifolia* and *G. aculeata*] have been cleared in recent decades for agricultural purposes." Unfortunately, bamboo stands were synonymous with "good banana land."

Past climatic changes may have decreased the distribution of the habitats available, as Toledo (1982) described in the changes undergone by the tropical forest in Mexico. Within the last 10,000 years there were times when the extent of the tropical forest must have decreased considerably, and bamboo habitats in southern Central America, where there are very few collections, may have been eliminated altogether. *Guadua angustifolia* is conspicuously absent in most of Nicaragua and in all of Costa Rica, and even though it occurs in North and South America, there are no collections from eastern Panama or lands bordering Panama in western Colombia. In contrast, *G. angustifolia* of Colombia and Ecuador has a broad ecological amplitude and can be found in lowland rainforest, lower montane rainforest, semideciduous forest, de-

ciduous forest, and savanna (Harling, 1979) as long as water is plentiful, and edaphic conditions are satisfactory. This ecological amplitude may have made the species more resistant to past climatic changes. Many areas of Central America where it could possibly occur have yet to be explored botanically, especially the Caribbean lowlands, and the species may thus be more common than maps would suggest. Standley (1931) described it as one of the conspicuous features of the landscape in the coastal regions of Guatemala and Honduras, being abundant in swamps and along rivers at low elevations, often forming extensive groves.

Another large disjunction occurs between eastern Colombia and the few specimens of southern Venezuela and Guyana. Its distribution in the Amazon basin remains very poorly known. The eastern populations can be found along many of the large rivers of the Ecuadorian Oriente, but just how far they continue into Peru and Brazil is unknown.

*Guadua angustifolia* is divided here into two subspecies separated by morphological differences (see taxonomic section) and occurring in widely separated geographic ranges (Figs. 2-4). Subspe-



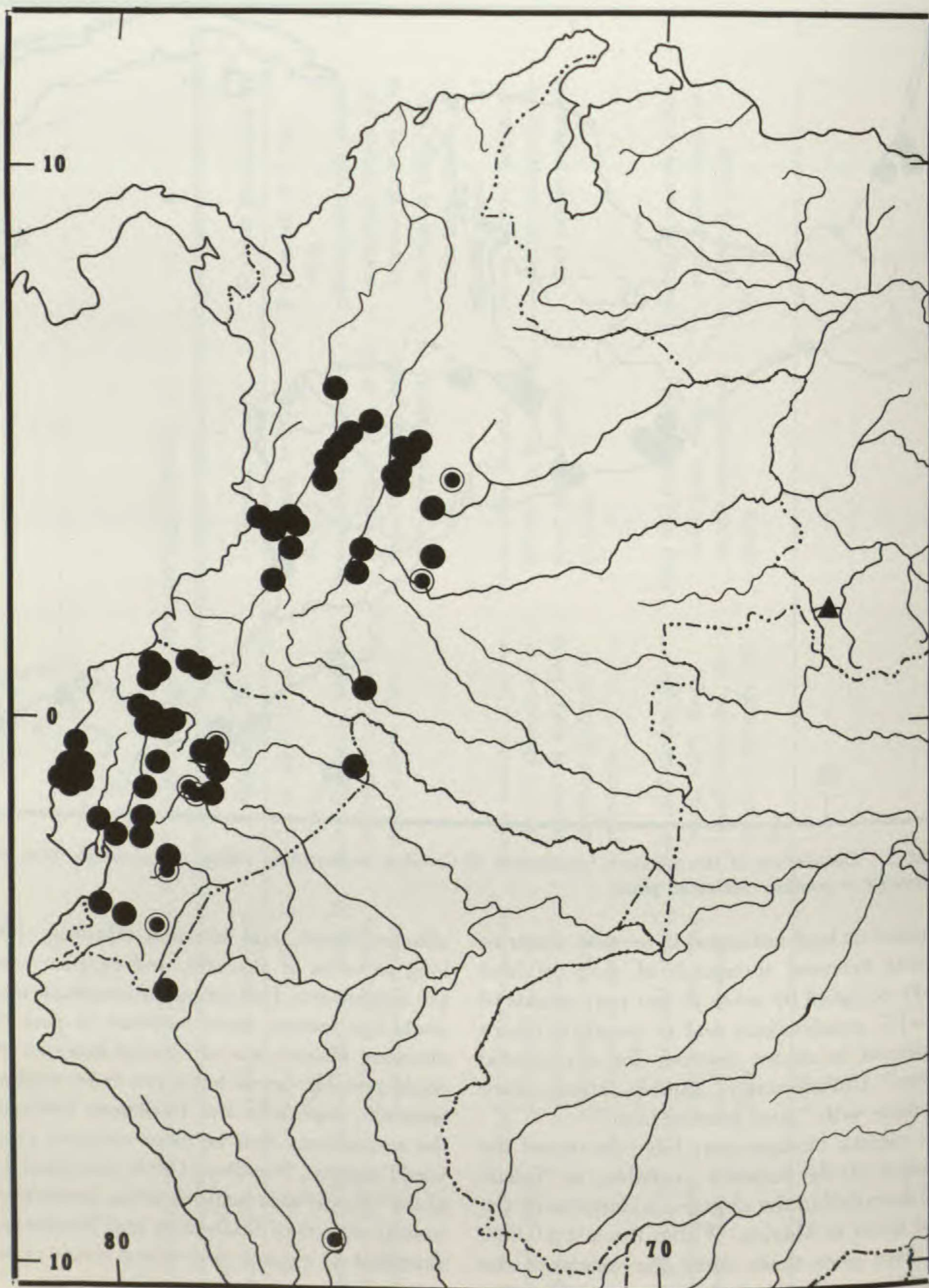


FIGURE 3. Distribution of western (dots) and eastern (dots in circles) populations of *Guadua angustifolia* subsp. *angustifolia*. Triangle = possible cultivated plant.

cies *angustifolia* extends into the northern Amazon basin of Peru, and subspecies *chacoensis* has its northernmost distribution in eastern Paraguay. Most of the specimens of *G. angustifolia* subsp. *chacoensis* have been collected along the Paraná and Paraguay rivers, but it is not known if the subspecies extends up these rivers into Brazil and if

so how far. In a study of bamboo-dwelling birds in southeastern Peru, Parker (1982: 483) reported, "It is interesting to note that close relatives of *Hemitriccus flammulatus*, the Flammulated Pygmy-Tyrant and *Sporophila shistacea*, the Slate-colored Seedeater (i.e., *Drymophila ochropyga*, Drab-breasted Pygmy-Tyrant and *Sporophila fal-*



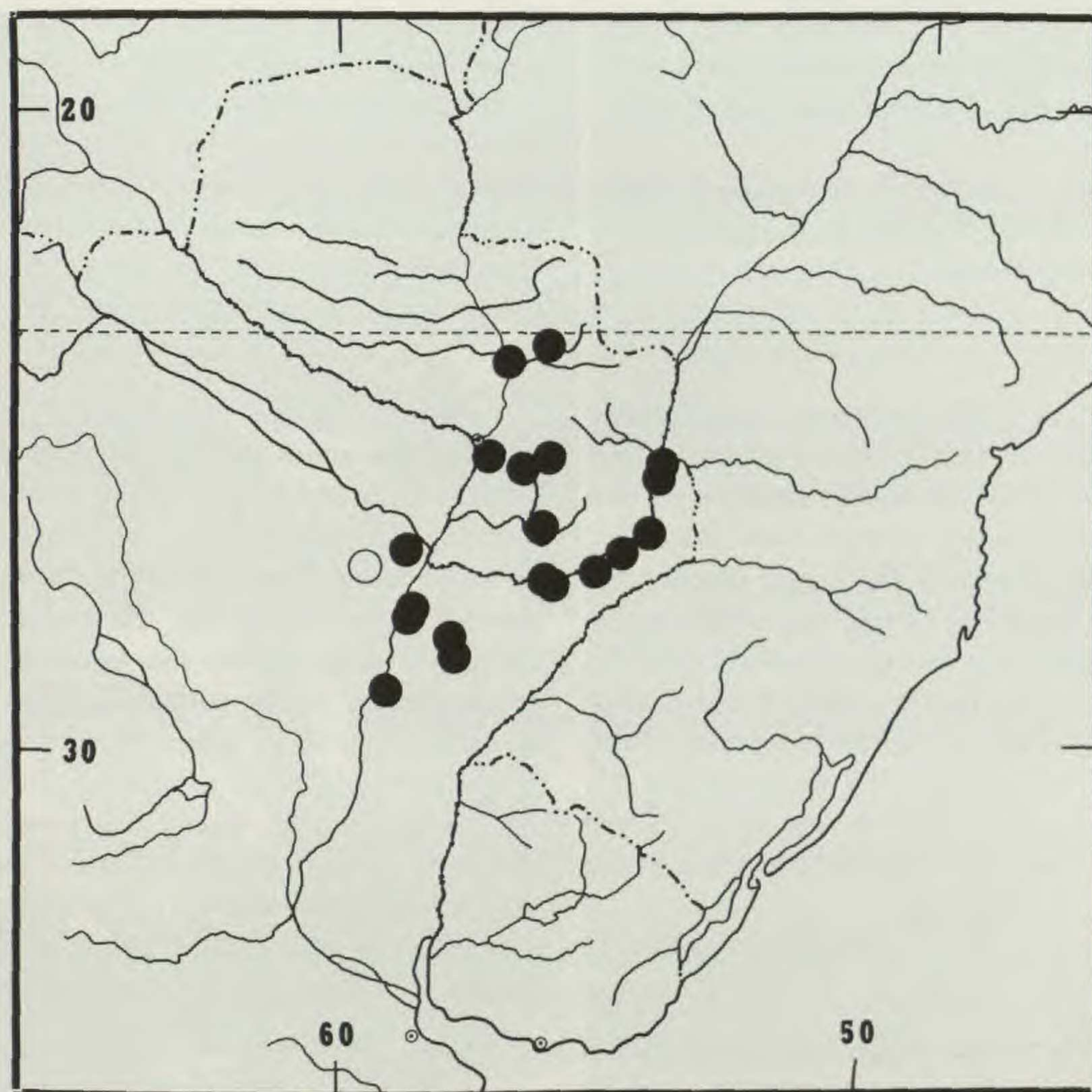


FIGURE 4. Distribution of *Guadua angustifolia* subsp. *chacoensis*. Open circle = unspecified locality in Chaco Province.

*cirostris*, Temminck's Seedeater) are found in bamboo in montane or subtropical areas from SE. Brazil to NE. Argentina. This suggests that certain bamboos were an important floristic element in a relatively cool, humid forest that may have once extended from the Andes to the Atlantic south of Amazonia proper." He listed eight other birds that are associated with bamboo and show similar disjunct distributions across the South American continent. Past climatic changes described by Prance (1982) lend credence to the setting up of a climatic barrier between the two regions. Future bamboo exploration in areas such as the Beni region of Bolivia or the southwestern regions of Brazil, and study of bamboo-animal associations, may yet reveal a former or even a present connection between the two subspecies.

Another unresolved problem is the role human cultivation has played in transporting these bamboos. The economic importance of *Guadua angustifolia* in pre-Columbian times is obscure although when the Spanish arrived in Colombia, they observed the native inhabitants using it in construction and wearing it as protective garb against

arrows (Farrelly, 1984). *Guadua angustifolia* has been and is being cultivated in many botanical gardens and agricultural experiment stations throughout Latin America. Some of the plants collected as wild have been suspiciously close to experiment stations and may be merely escapes; *G. angustifolia* plantings are known from southern Brazil to southern Florida.

#### TAXONOMIC CRITERIA

Collecting difficulties have always hindered the detailed study of large woody bamboos. Most of the plant parts, aside from foliage leaves and spikelets, are too large to be easily gathered, pressed, or transported. The combination of a hot tropical climate, elephantine plant size, and masses of thorny branches is usually enough to deter even the most intrepid botanist from collecting these woody grasses unless the plants are flowering. Complete collections that include many of the vegetative parts of a bamboo have proven just as valuable in identification as specimens with floral parts (McClure, 1966; Soderstrom & Young, 1983). Unfortunately,



ly, herbarium specimens containing only foliage leaves far outnumber those containing culms, culm leaves, and branches. Rhizomes are almost never collected.

The taxonomic usefulness and variation within the characters of the *Guadua angustifolia* complex are discussed below.

#### RHIZOMES

*Guadua angustifolia* possesses pachymorph rhizomes (McClure, 1966). These rhizomes are composed of two parts—the neck, a narrow portion where internodes do not possess buds (Fig. 5a), and the rhizome proper, a thick part where buds are present at the nodes. In *G. angustifolia*, the neck is elongated and positively geotropic so it first grows down from the rhizome proper to form prop-like structures before giving rise to another short, swollen, fusiform rhizome. The shape of the rhizome and accompanying necks has been likened to an alligator, and the rhizomes are often called *caimán* by locals (Fig. 6a).

#### CULM INTERNODES

The culm internodes of *Guadua angustifolia* differ from all other species of the genus *Guadua* mainly in diameter, length, and wall thickness. Culms of *G. angustifolia* have the largest diameters of any of the species (Fig. 6b), and the wall is of medium thickness (Fig. 6c) with the basal internodes being the shortest and the most thick-walled. The length of the internode and its variation in length and diameter from base to apex is rarely measured. Internode length at the basal 2 m of the culm usually does not exceed 30 cm. The lumen is often filled with potable water and sometimes contains insects or insect larvae (Fig. 7a). The sulcus above the branch bud usually does not extend beyond mid-internode, although it may be perceptible along the entire length.

Hairs cover the surface in varying densities. They are usually sparse and do not obscure the surface (Fig. 5b), or they may be entirely absent.

These hairs are deciduous and leave distinct impressions in the culm surface.

During the first two years of growth the internodes are dark green but then become gradually lighter green and covered with lichens (Fig. 5d). As in most bamboos, when the culms die they turn from green to tan. No studies have been done on the life span of individual culms.

#### CULM NODES

The culm nodes of *Guadua angustifolia* do not differ significantly from many other species in *Guadua*. Most species have a characteristic band of white hairs extending from the nodal ridge to the nodal line and below the nodal line for 1–3 cm. In *G. angustifolia* this band of hairs is very prominent on young culms (Fig. 5c), but may be partially worn off or obscured with age. The nodal ridge is often difficult to observe, but its presence can be felt with the hand. This prominence varies within *G. angustifolia* from easily seen to absent. The interior nodal wall may be convex or horizontal and varies in different diameter culms (Londoño & Prieto, 1983).

#### CULM LEAVES

Culm leaves are one of the most useful vegetative characters in separating taxa and are used here in separating subspecies. Because the culms of *Guadua angustifolia* are large, the culm leaves are also large (Fig. 7b) and often must be folded over to fit into a plant press. They surround and protect the newly developing culm and, like the internodes they cover, vary in size and shape from the base to the apex of the culm (Fig. 9a). At the base they are usually as long as they are wide, and toward the apex the leaves become progressively longer and more narrow, and the blade makes up a larger percentage of the whole leaf.

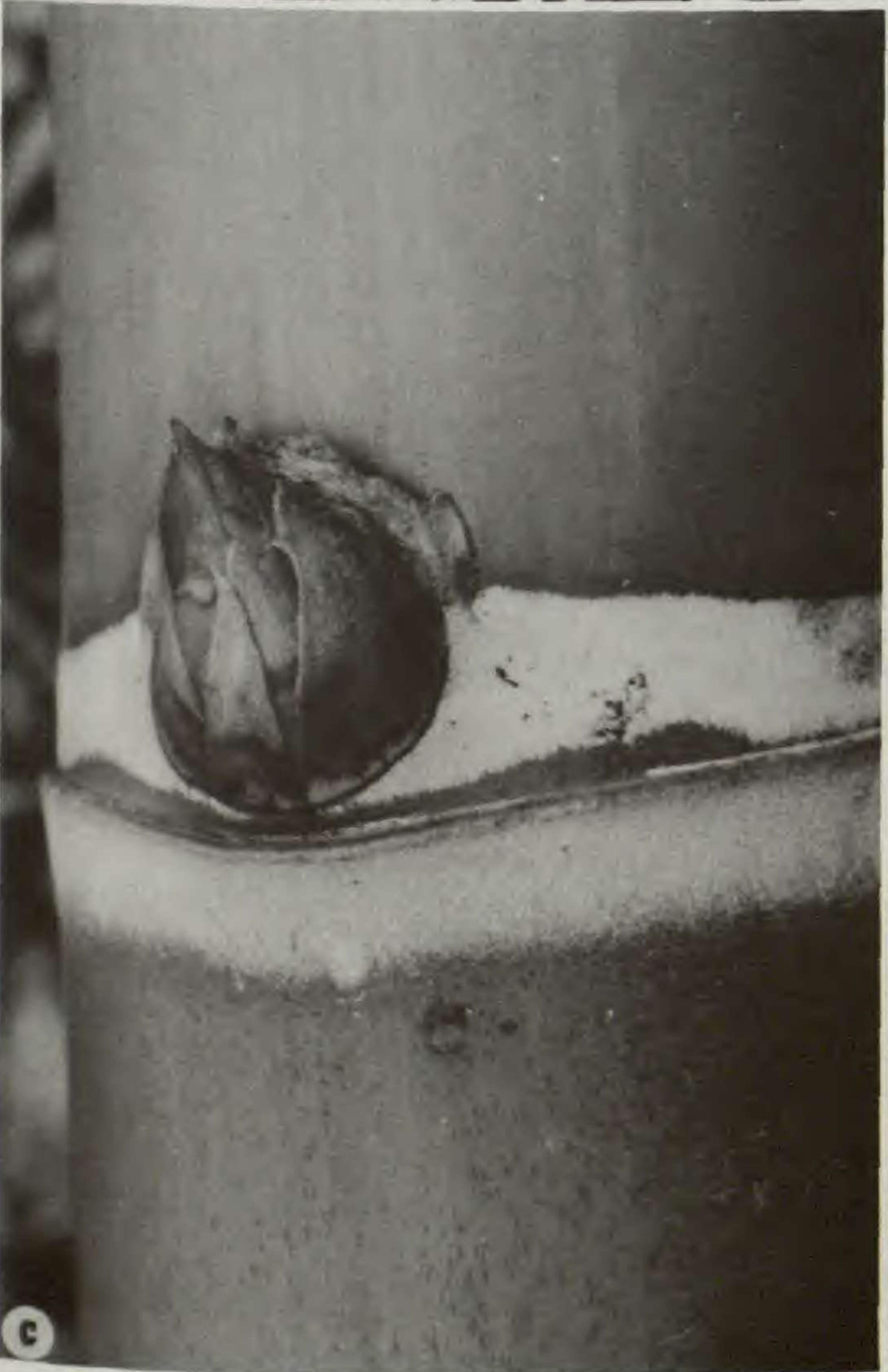
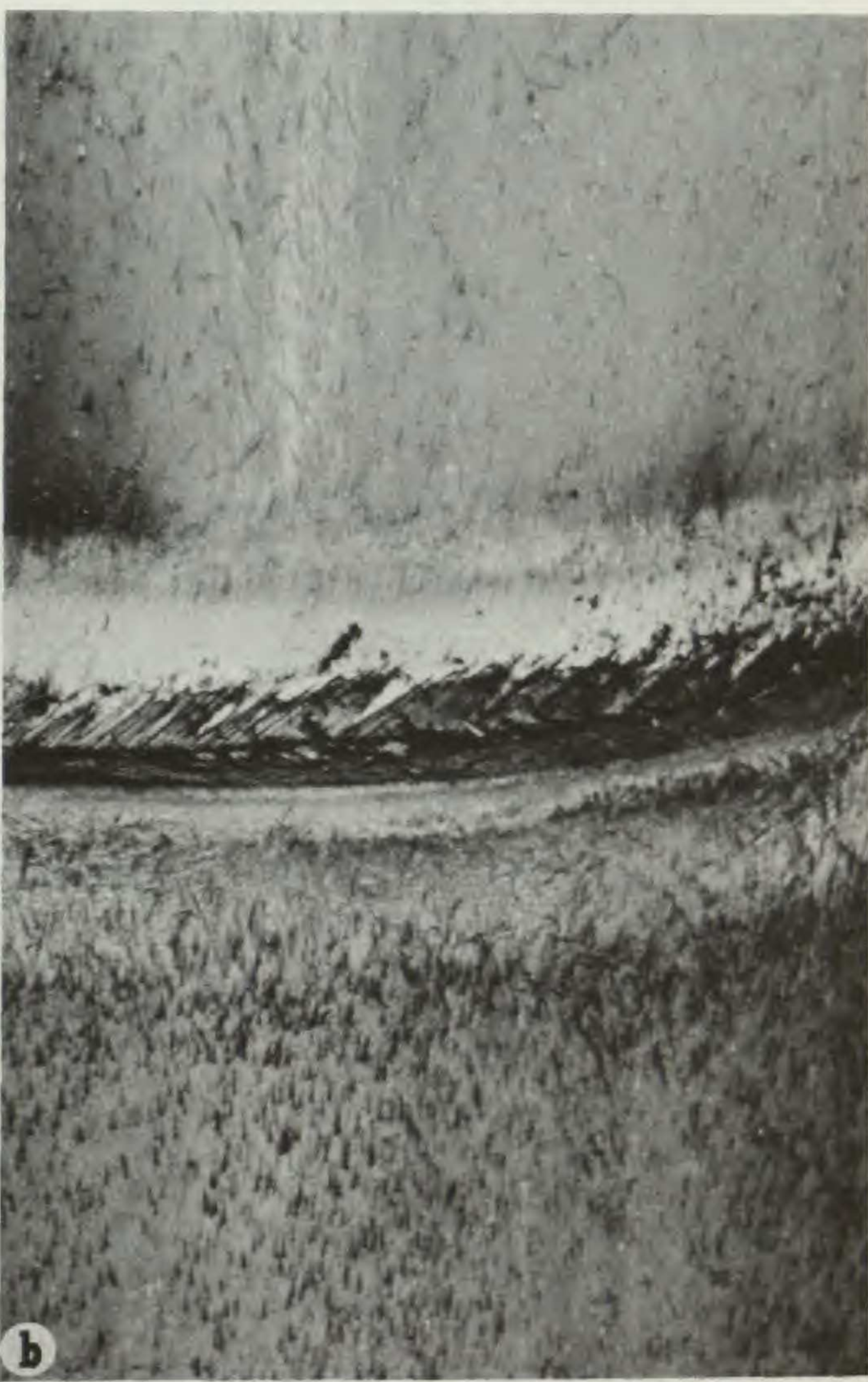
The shape of the ligule in *Guadua angustifolia* subsp. *angustifolia* varies within the same plant but is most often convex in the center. The ligules almost always turn up and end a few millimeters

FIGURE 5. Vegetative morphology of *Guadua angustifolia* subsp. *angustifolia*.—a. Long rhizome necks extending down from rhizome.—b. Stiff hairs on internodes.—c. Nodal region and bud.—d. Lichen-covered culm.

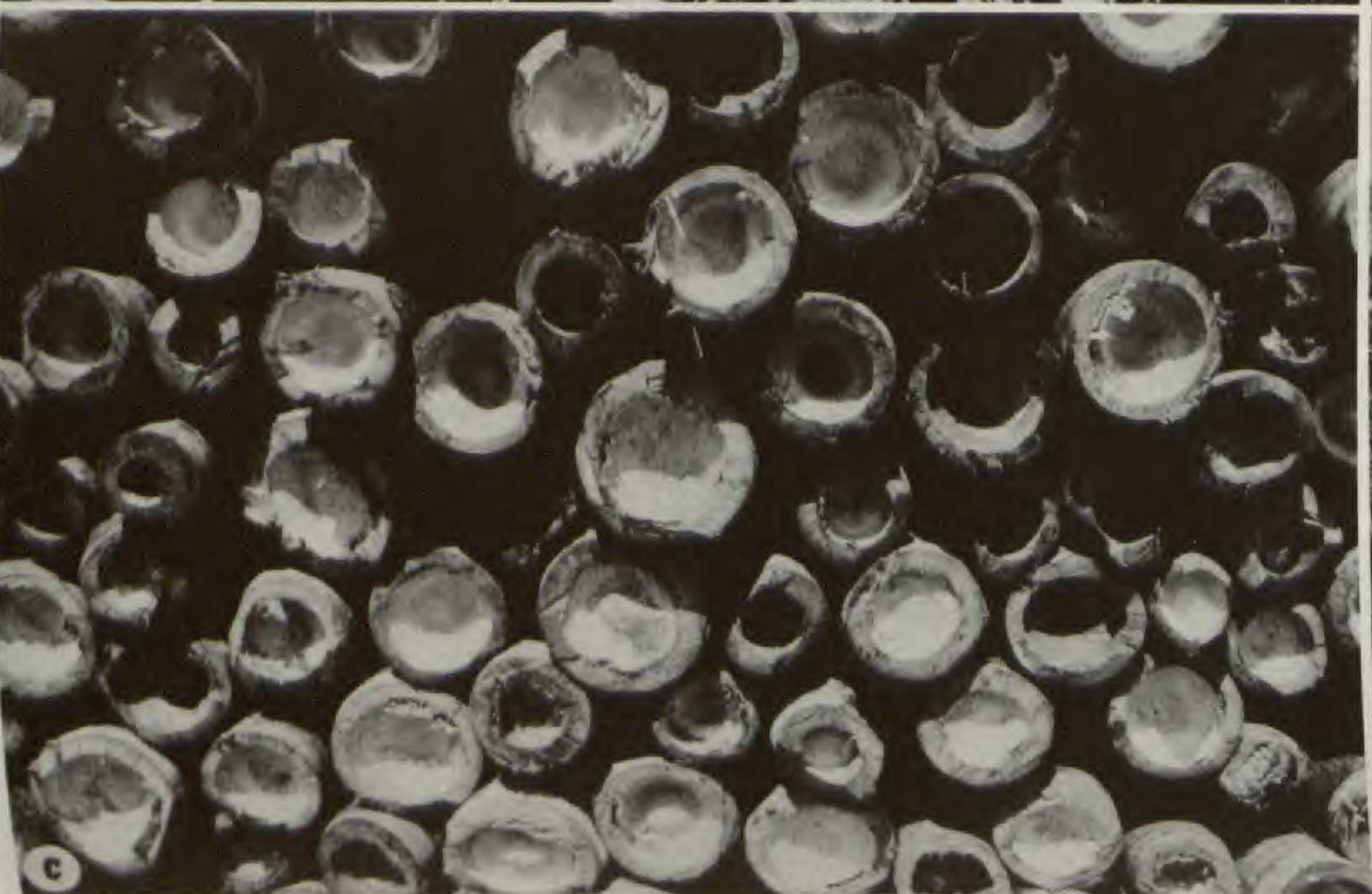
FIGURE 6 (p. 752). Vegetative morphology of *Guadua angustifolia* subsp. *angustifolia*.—a. Pachymorph rhizomes.—b. Cutting a large diameter culm from Chicolá, Guatemala (photo F. A. McClure).—c. *Guadua* culms showing medium wall thickness and lumen.—d. Culms with no basal branches, Chinchiná River, Colombia (photo F. A. McClure).

FIGURE 7 (p. 753). Vegetative morphology of *Guadua angustifolia* subsp. *angustifolia*.—a. Larvae of microlepidopterous insect found inhabiting the internode of a culm, Chicolá, Guatemala (photo F. A. McClure).—b. Large culm leaf from Chuchumbeza, Zamora-Chinchipe, Ecuador.—c. Upper branches developing in young culm.—d. Lower branches developing from culms, Coatepeque, Guatemala (photo F. A. McClure).

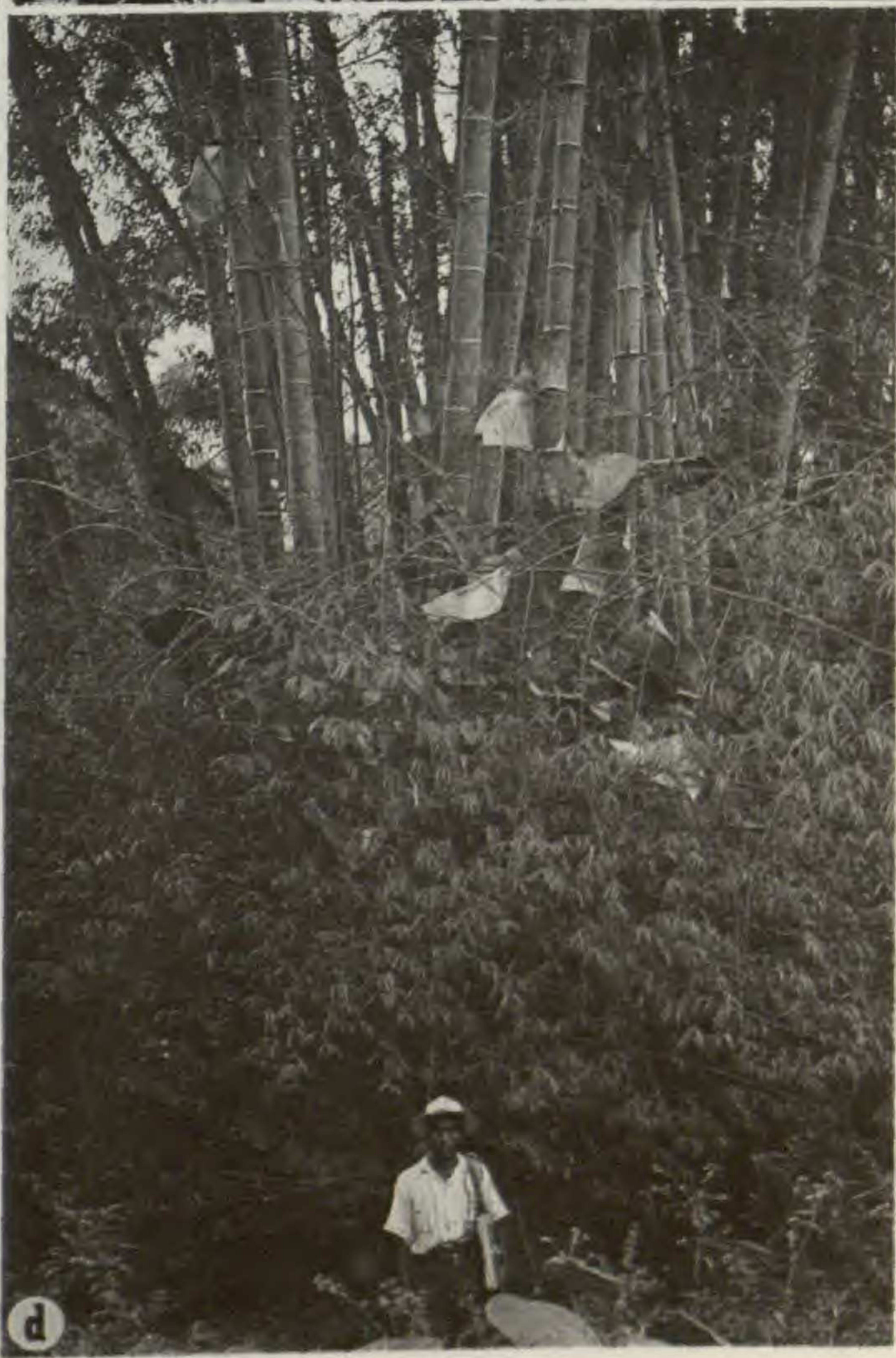
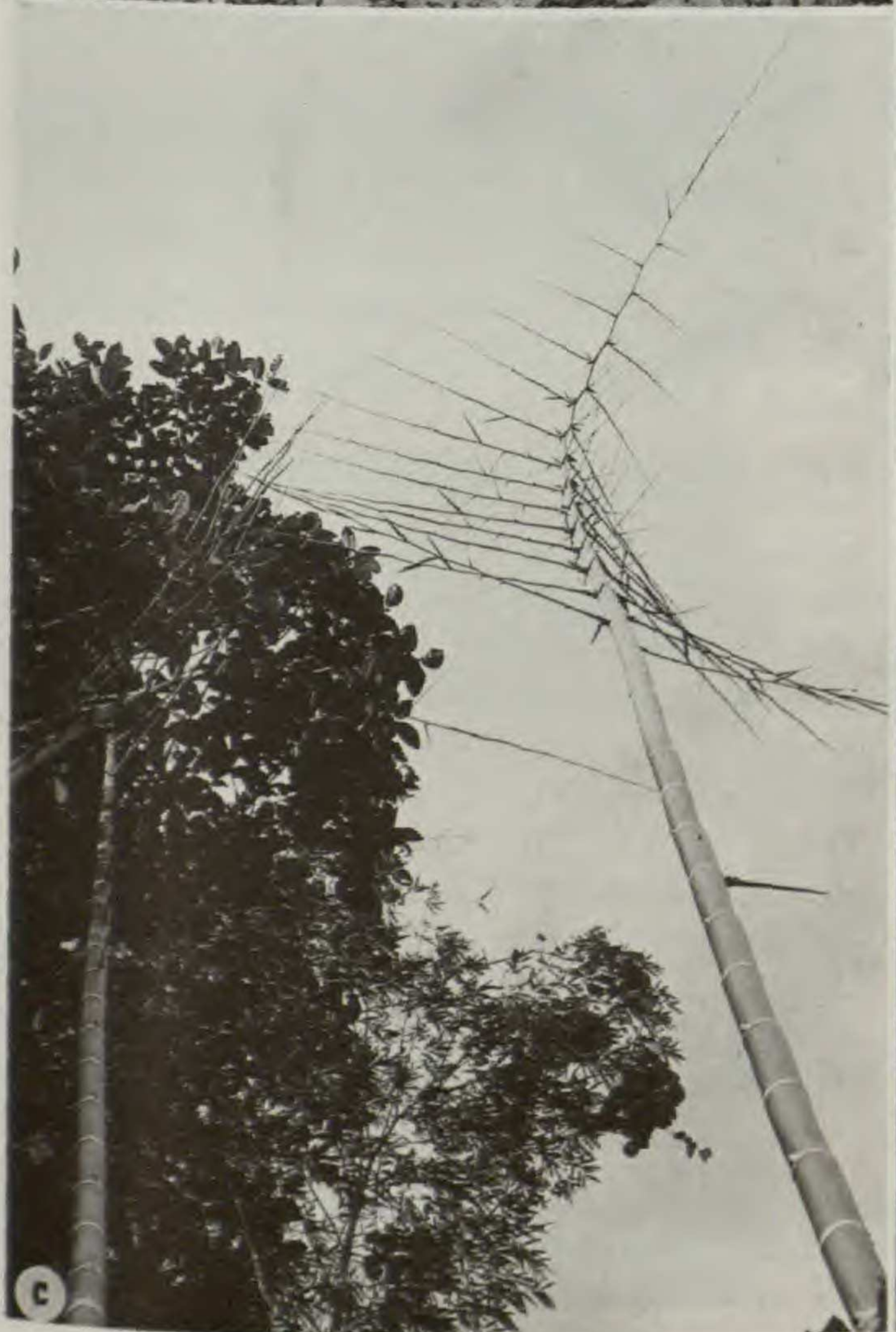


















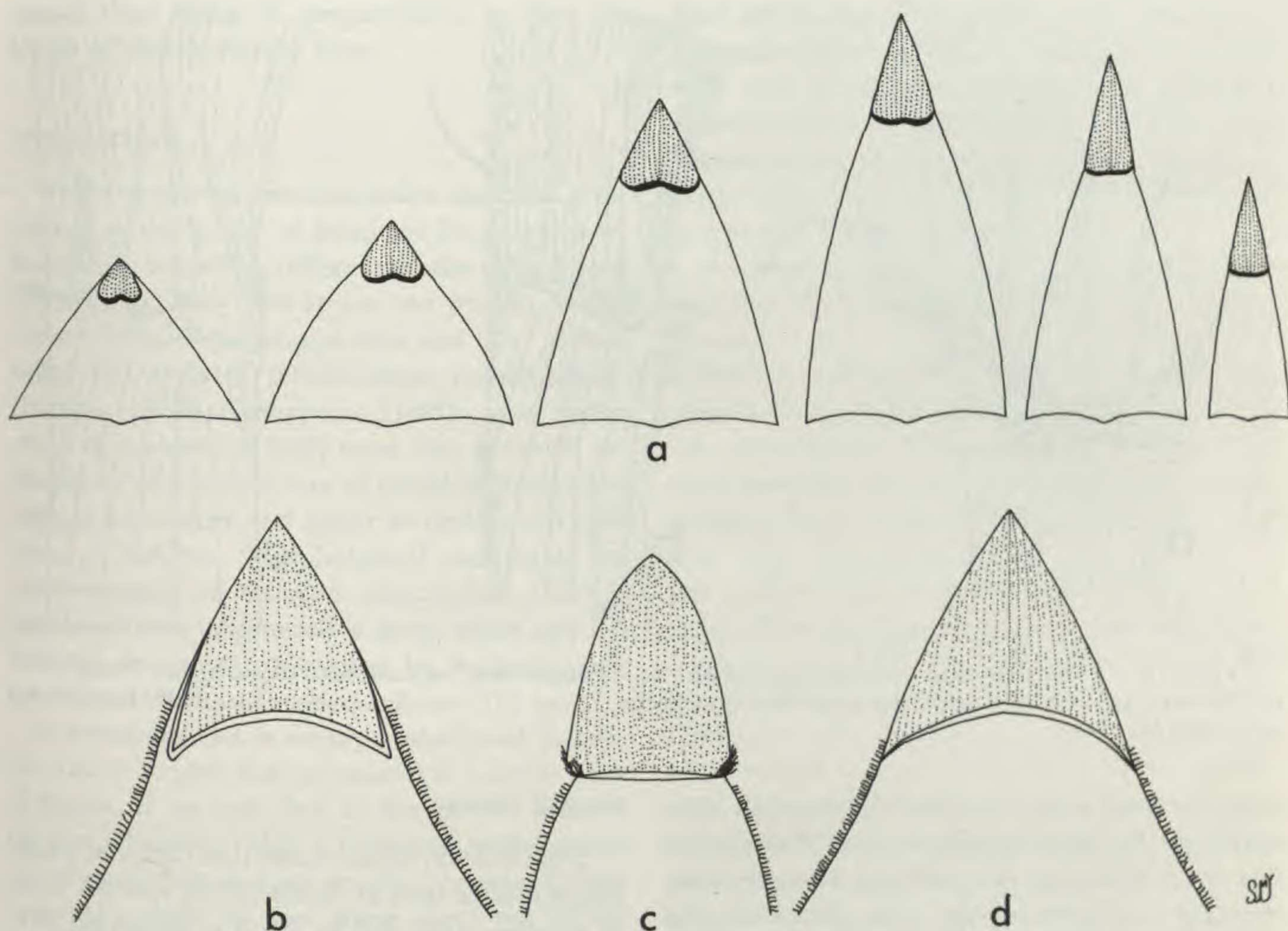


FIGURE 9. Culm leaves of *Guadua angustifolia*. —a. Culm leaf variation within the same culm (left to right = base to apex of culm). —b. Ligule of lower culm leaf of *Guadua angustifolia* subsp. *angustifolia*; McClure 21401-21403. —c. Ligule of culm leaf near apex of culm of *G. angustifolia* subsp. *angustifolia*; McClure 21737. —d. Ligule of culm leaf of *G. angustifolia* subsp. *chacoensis*; Krapovickas et al. 25470.

before the margins (Fig. 9b). Apical culm leaves may have ligules that are continuous to the margin and have groups of oral setae present there (Fig. 9c). *Guadua angustifolia* subsp. *chacoensis* is distinguished by having ligules that are often continuous to one or both margins in the lower culm leaves, but no oral setae are present as in *G. angustifolia* subsp. *angustifolia* (Fig. 9d). The hairs on the margin of the ligule are also less dense and longer in subspecies *chacoensis* than in subspecies *angustifolia*. Auricles are not present in *Guadua angustifolia*, and the blade comprises only a small percentage, usually less than 20%, of the total leaf length.

Hairs covering the abaxial side of the leaf vary from dense to sparse, and their position on the leaf also varies a great deal. These hairs are long and

straight to short and contorted and vary from black or brown to golden in the longer hairs and to white in the shorter hairs. The longest hairs are stiff, sometimes branched, and sharp-pointed. They are readily detached.

The culm leaves are caducous and usually can be found within the clump in good condition for pressing. The blade is erect and stays firmly attached to the sheath. Leaves at the base of the culm remain attached for a longer period of time than those from farther up the culm and may disintegrate in place.

#### BRANCHES

Branching patterns do not vary significantly within *Guadua angustifolia*, although the position

FIGURE 8. Vegetative morphology of *Guadua angustifolia* subsp. *angustifolia*. —a. Branching from middle portion of culm, Chocolá, Guatemala (photo F. A. McClure). —b. Branch from lower culm developing as a large thorn, Río Palenque Biological Station, Ecuador. —c. Culms along Cayapas River, Esmeraldas, Ecuador. —d. Culms with no basal branches, Escondido River, Nicaragua.



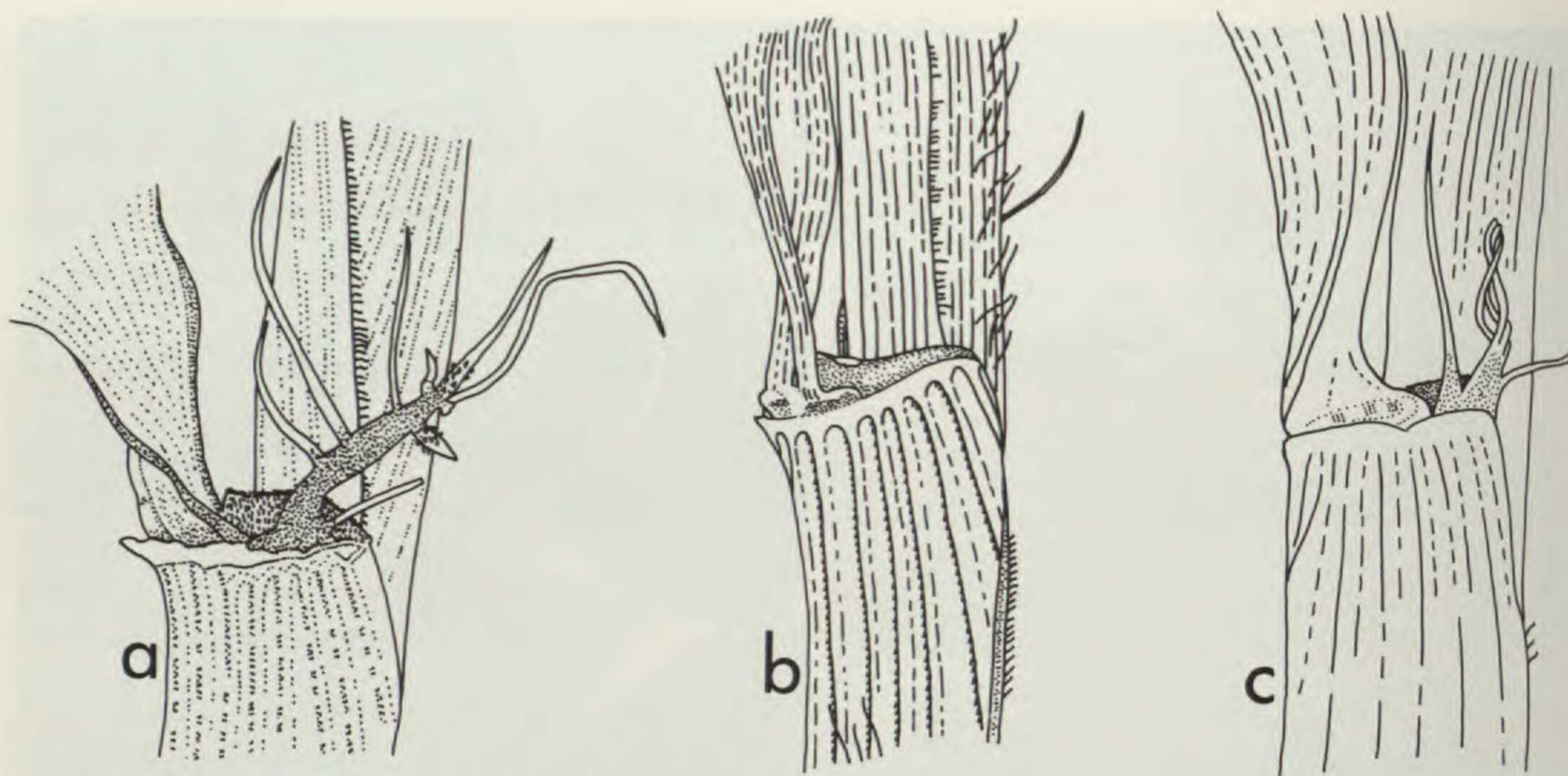


FIGURE 10. Foliage leaves of *Guadua angustifolia*. —a. "Eastern race" of subspecies *angustifolia*; Young 92. —b. "Western and northern race" of subspecies *angustifolia*; Young 117. —c. Subspecies *chacoensis*; Krapovickas et al. 25470.

along the culm where branches develop does show variation. One main branch develops from a single bud at the node (Fig. 5d), and while branches from the upper one-third of the culm always develop (Fig. 7c), the development of the lower branches varies. The development of branches in the lower third of the culm is common (Fig. 7d), but in certain areas within its geographic range most of the culms of *G. angustifolia* do not possess lower branches (Figs. 6d, 8d). Most of the culms observed by the first author in the province of Esmeraldas, Ecuador (Fig. 8c), were devoid of lower branches until a culm was cut. Then, one of the lower buds broke dormancy to produce a very thorny lateral branch. This characteristic will remain of doubtful taxonomic significance until additional studies are made.

The closely set nodes at the base of the branches contain buds that remain dormant or produce one or two secondary branches which may again branch (Fig. 8a). These higher-order branches may develop as thorns or elongate into normal vegetative branches. While the upper branches may be thorny or thornless, the lower branches, when they develop, always possess thorns. The main branch may develop only slightly and produce one large thorn (Fig. 8b) or it may rebranch and develop one to four additional thorns at its base. There do not seem to be consistent differences in thorn development within *Guadua angustifolia*, and the taxonomic usefulness of this character is negligible.

Branch internodes and nodes are covered with hairs similar to the culm internodes but their caducous nature makes them of little taxonomic use.

#### FOLIAGE LEAVES

The variation in structures that comprise foliage leaves is often used in distinguishing species. Within *Guadua angustifolia* there is significant variation in foliage leaves as well as culm leaves, and care must be taken in selecting average leaves when comparing taxa. Within one plant, for example, leaf size may vary considerably since the first leaves to appear on a branch (juvenile leaves) are longer and wider and have slightly different indumentum than subsequent leaves. When these juvenile leaves are the most abundant and most accessible leaves on the culm they are sometimes the only ones included in a collection. New leaves may also develop to a smaller size when flowering takes place because they gradually decrease in size toward the spikelets. Leaves closest to the spikelets fail to develop their blades altogether and become the gemmiparous bracts of the pseudospikelet.

Particular characters of the leaf that are taxonomically useful are leaf size, leaf sheath indumentum, oral setae number, presence of auricles, outer ligule size, inner ligule size and indumentum, pulvinus size, and blade and petiole indumentum (Fig. 10). All of these vary somewhat between primary and subsequent leaves.

Hairs and the marginal rows of prickle-hairs were examined on the blade. The number of rows of prickle-hairs varied a great deal within *Guadua angustifolia*, but their presence may prove useful in separating this species from others within the genus. Petiole length also varies more between



species than within *G. angustifolia*, as does the length of sheath margin hairs.

#### INFLORESCENCE

The structure of pseudospikelets has been problematic in this group of bamboos because the inflorescence branching differs from the typical grass spikelet. McClure (1934) was the first to discuss the structure of pseudospikelets and later (1966) called this type of inflorescence indeterminate. Holttum (1958), Soderstrom (1981), and Soderstrom & Londoño (1988) have also provided explanations of the structure of pseudospikelets that seem to be clearer and easier to understand than those of McClure. Morphological analysis of the synflorescence of *Guadua angustifolia* (and of pseudospikelets in general) is given below and follows the description developed by Soderstrom & Londoño (1988).

A pseudospikelet is simply a shortened vegetative axis or branch that terminates in a single spike of florets. If we look first at the growth form of the entire bamboo culm, it originates underground as a rhizome branch from another rhizome. It then eventually turns up and grows erect out of the ground and is called a culm. From the main culm an alternate, monopodial pattern of branches develops from the nodes with each successive branch becoming smaller until the sequence stops at the smallest twigs. Each branch is subtended by a leaf or bract and begins with a double-keeled leaf called a prophyll. The prophyll and subtending bract for the main culm (a branch from a rhizome) is underground where it branches from another rhizome (Fig. 11a).

When flowering occurs, the vegetative twigs elongate to varying lengths beyond the foliage leaves and terminate in a series of one to four short vegetative internodes followed by a single spikelet, the main florescence. Additional flowering branches or paracladia may also arise from vegetative buds farther down the branch (Fig. 11b, c).

The short uppermost internodes of these flowering branches are vegetative and contain one to several vegetative buds. These buds are subtended by modified leaves called gemmiparous bracts, which resemble the lemmas, making that part of the branch appear as part of the spikelet. The vegetative branch segments bearing the gemmiparous bracts and the spikelet proper are together called the pseudospikelet (Fig. 12a).

When flowering begins, the pseudospikelets that develop at the apex of branches have the same prophylls and subtending bracts as the branches

from which they develop (Fig. 12a). Therefore, if a pseudospikelet develops at the apex of the main culm axis, its prophyll and subtending leaf will be underground at the junction of the rhizomes. Pseudospikelets that develop from the nodes of branches begin with a prophyll and are subtended by a leaf or bract at the base of the branch.

As flowering continues, each bud within a gemmiparous bract may develop into another shortened vegetative axis, a paracladium, terminating in a spikelet or cincinnus. This sequence may proceed to form a ball of pseudospikelets, but in *Guadua angustifolia* usually only two or three shortened branches develop close together to form a synflorescence, or the buds may not develop at all (Fig. 12b). The pseudospikelet that gives rise to this synflorescence is here called the main florescence. The main florescence is usually the largest one and is used for comparison among taxa since pseudospikelets of further cincinni gradually diminish in size. The length of branches and distance between internodes varies in each complement of branches, and it is often difficult to delimit a "cluster" in a nonarbitrary fashion. If pseudospikelets were separated by an internode of less than 1 cm, they were considered part of the same cluster, containing a main florescence and associated cincinni. If two pseudospikelets were separated by an internode of more than 1 cm, they were considered to be two distinct synflorescences. The above distribution is made arbitrarily and only for convenience, since all spikelets are terminal to a vegetative branch.

When the vegetative portion of the branch becomes reproductive, buds along the axis, now called the rachilla, develop into florets consisting of a short axis beginning with a prophyll called the palea. The axis terminates in a flower consisting of three lodicules, six stamens, an ovary, style, and three stigmas. The axis is subtended by a bract called the lemma.

We found no budless bracts (glumes) between the gemmiparous bracts and the lemmas, although they have been observed in other species. Sometimes there were no gemmiparous bracts at all on the branch, especially in cincinni, and florets began immediately distal to the prophyll. The prophyll may subtend a bud but is almost always empty. Once a bud develops at a node, the subtending bract is quickly deciduous and is almost never found.

The short axis (here called the peduncle) between the vegetative portion of the branch and the floral portion does not branch before it becomes part of the spikelet (Fig. 12).



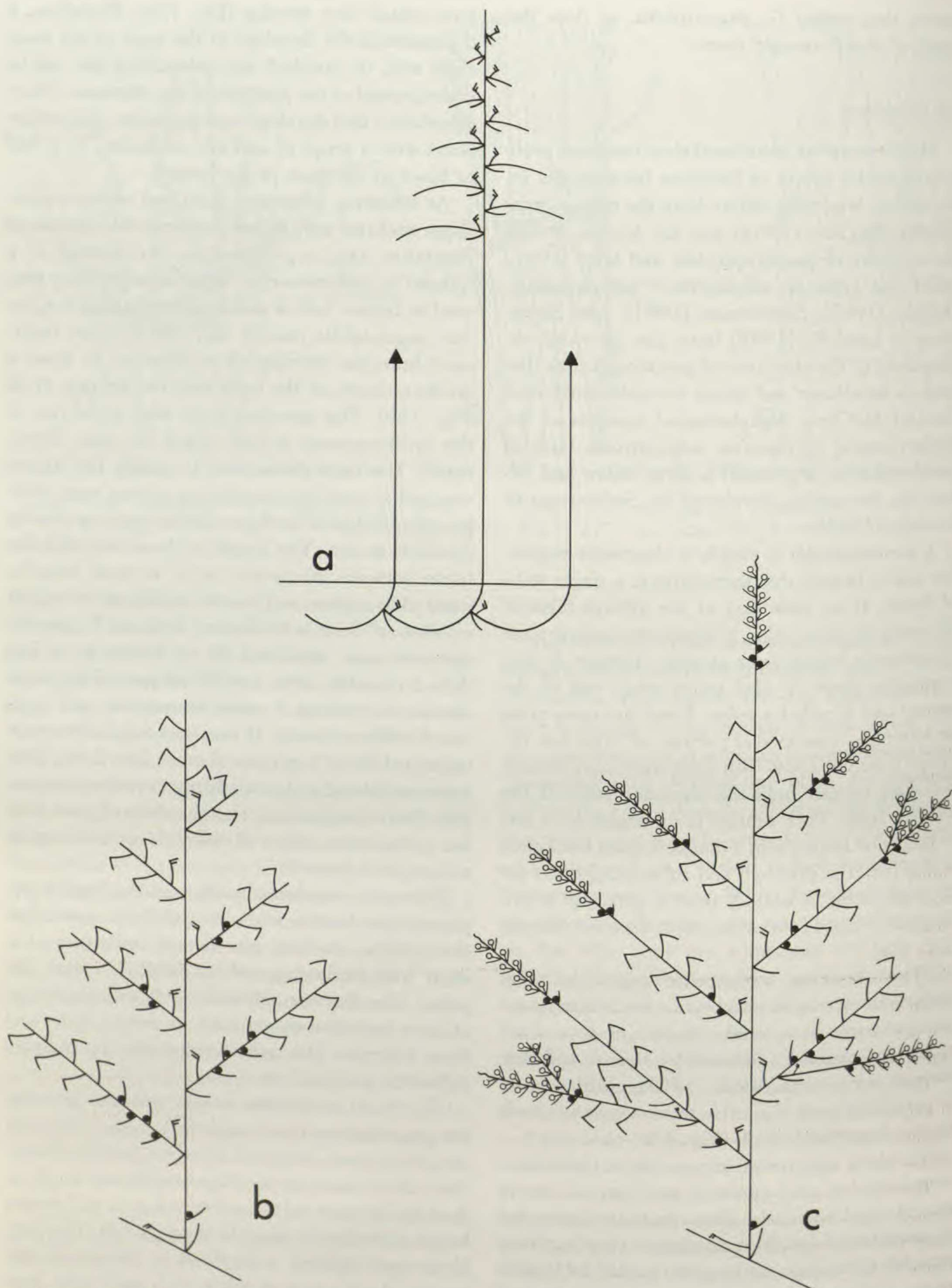


FIGURE 11. Culm and inflorescence development in *Guadua angustifolia*.—a. Culm development and branching.—b. Vegetative leafy branch.—c. Synflorescence developing as an extension of a twig or from lateral buds. Stalked open circle = fertile floret; solid circle = vegetative bud; double-barreled flag = prophyll; curved line with hanging tip = branch leaf sheath and blade, respectively; curved line alone = subtending branch leaf or bract, gemmiparous bract, lemma, or glume; wiggly line = terminal aborted part of axis.



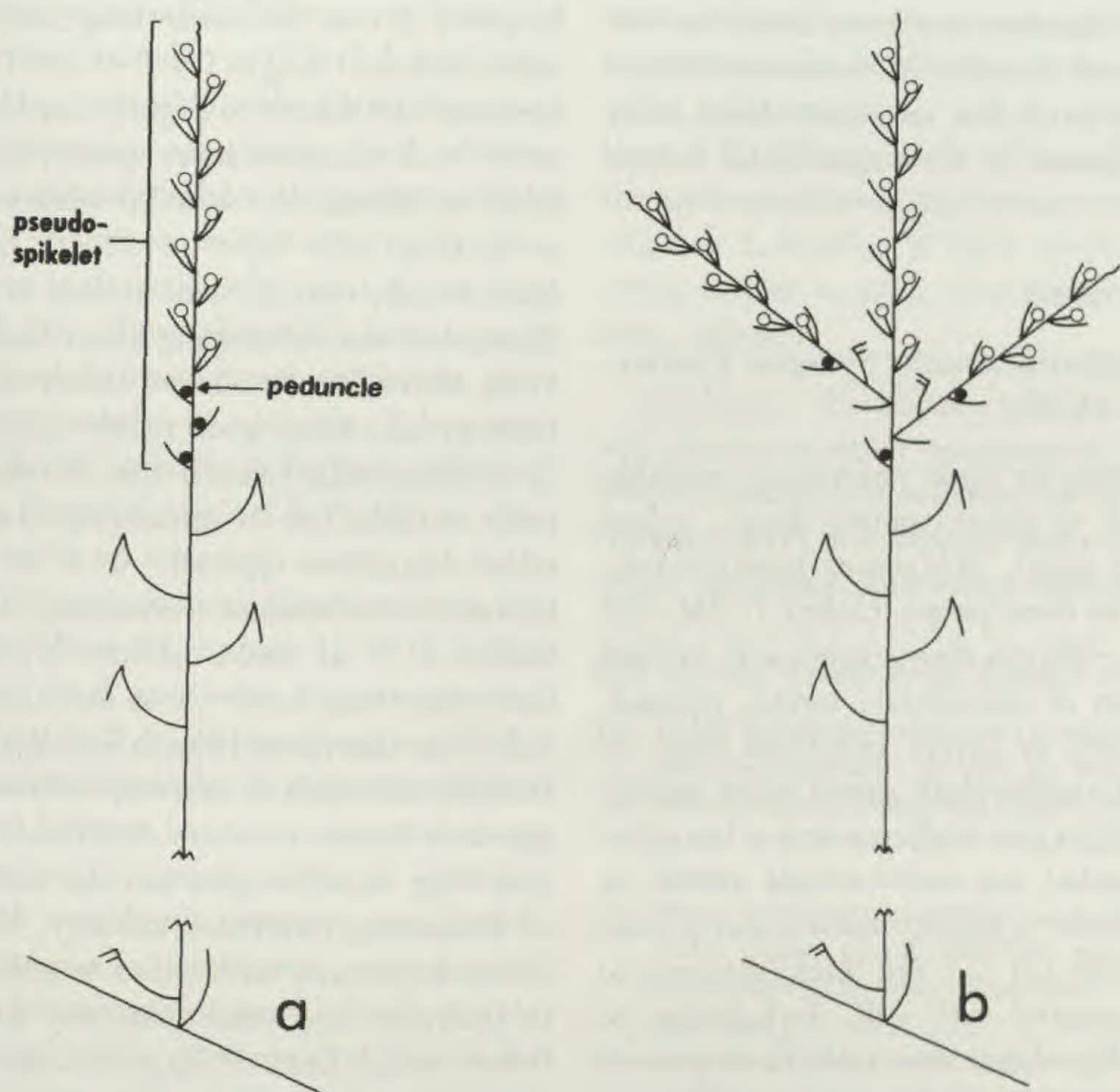


FIGURE 12. Pseudospikelet morphology in *Guadua angustifolia*. —a. Main florescence. —b. Branching of vegetative buds of main florescence to form a synflorescence of one main florescence and two colflorescences. Stalked open circle = fertile floret; solid circle = vegetative bud; double-barreled flag = prophyll; curved line with hanging tip = branch leaf sheath and blade, respectively; curved line alone = subtending branch leaf or bract, gemmiparous bract or lemma; wiggly line = terminal aborted part of axis.

In order to standardize measurements, the first author measured the characteristics of the uppermost gemmiparous bract and lowermost floret of terminal pseudospikelets, and the first rachilla segment between the lowermost floret and the one distal to it. The vegetative axis was measured between the uppermost gemmiparous bract and the one below it and was called the "uppermost vegetative internode."

The gemmiparous bracts often differed slightly in indumentum characteristics and color from the lemmas. They were sometimes more pubescent and lighter in color.

The lowermost florets develop first, and those formed subsequently gradually become smaller toward the apex as in a typical racemose inflorescence. The size of the ovary decreases between the proximal and distal florets within a spikelet, and the uppermost two or three florets possess only rudimentary stamens.

Many spikelets examined had already undergone anthesis, and the anthers had become detached from the filaments. This gave the impression that the lowermost florets were carpellate, especially

since the filaments are very delicate and difficult to observe.

External inflorescence characters are more useful than characters from dissected pseudospikelets when comparing populations within *Guadua angustifolia*. The physical dimensions of the pseudospikelets (i.e., length, width, stature) and the number of florets per spikelet are the most useful external characteristics. The presence of leafy branches intermingled with the pseudospikelets is not consistent in Central America but tends to be a more reliable distinction between the subspecies in South America. Indumentum characteristics of the pseudospikelets are important in distinguishing *G. angustifolia* from other species of the genus, but they are less valuable within the species itself. However, a few internal inflorescence characters, i.e., palea length, style length, and style hair length, proved helpful in distinguishing populations.

#### CHROMOSOMES

Quarín (1977) reported a somatic chromosome number of  $2n = 46$  for *Guadua angustifolia* subsp.



*chacoensis*. This number has been found in two additional species of *Guadua* (*G. capitata* Munro and *G. paraguayana*), but no counts have been taken from any plants in *G. angustifolia* subsp. *angustifolia*.

#### TAXONOMIC TREATMENT

***Guadua angustifolia* Kunth**, Synopsis Plantarum 1: 253. 1822.

*Clump* caespitose to open caespitose, variable in extent from 5 to many meters diam., culms arising 0.5–2 m apart. *Rhizomes* pachymorph, necks elongated to form props. *Culms* 7–25(–30) m tall and 7–15(–20) cm diam., erect with arched tops; indumentum of unicellular, terete, pointed, hollow, unbranched or rarely branched hairs or prickly-hairs. *Internodes* dark green when young, turning green to light green when mature, but some forms with irregular, narrow, vertical yellow or white stripes, sulcate to slightly sulcate above buds and branches; walls 1.5–2.5 cm thick; glabrous to rarely densely covered with stiff, dark brown to black, occasionally white, antrorsely or retrorsely oriented hairs, 0.1–2.5 mm long, often deciduous and leaving imprints, and usually increasing in density toward apex of culm. *Nodes* solitary; surface densely covered with white, cream, or golden brown, variously oriented hairs 0.1–2 mm long and extending 1.5–2.5 cm below node, loosely attached, and sometimes lacking on older culms; nodal line prominent; nodal ridge inconspicuous to absent. *Culm leaves* deciduous but usually persistent at lower nodes, sheath and blade falling together, size varying with position on culm, (18–)20–70(–78) cm long and (9–)10–50(–55) cm wide at sheath base, average leaf 36 cm tall and 32 cm wide; *sheath* stiff, dark to light brown, adaxially densely to sparsely covered with white to light brown, twisted hairs 0.1–0.4 mm long, and densely covered to lacking, light to dark brown or black, straight, stiff, rarely once-branched, deciduous hairs 0.5–2.3 mm long, the larger hairs usually prostrate and antrorsely oriented, the margins entire with scattered, stramineous to brown hairs measuring 0.5–4.0 mm long, the auricles lacking, the oral setae sometimes present at junction of sheath and blade margins in culm leaves from upper culm, the ligule commonly convex at center, sometimes straight, ends usually curved up before reaching leaf margin, sometimes continuous to one or both margins, with entire margin fringed with hairs measuring 0.1–0.5 mm long; *blade* stiff, triangular, erect, persistent, dark to light brown or grayish brown, (1.5–)2–14.5(–15.5) cm long, average

length 7.2 cm, the blade length as a ratio to the total culm leaf length 0.07–0.23:1, the base continuous with sheath to slightly cordate, the margins entire with marginal hairs usually scattered toward base or absent, the abaxial surface covered with or lacking both types of sheath hairs, but large hairs usually only present at base or along margins. *Branches* not developing from buds along center  $\frac{1}{3}$  or lower  $\frac{2}{3}$  of culm or rarely developing from buds at all nodes, buds rarely absent from center  $\frac{1}{3}$  of culm; main branch one, developing intravaginally at nodal line or remaining as a thorn; higher-order branches typically 0–4 at base of other branches, sometimes remaining as 1–4 thorns; thorns 1–5 at node, almost always present on branches from lower  $\frac{1}{3}$  of culm, upper branches thorny or thornless; branch internodes thick-walled to solid, the surface sparsely covered with or lacking dark brown to white deciduous hairs, 0.1–2.5 mm long; branch nodes in close succession at base of branches, otherwise solitary, the surface glabrous to covered with white to golden brown hairs to 0.2 mm long, and that may extend to 5 mm below nodal line. *Foliage leaves* 2–8(–12) per complement; *sheaths* stramineous to light brown, rarely marked with purple along margins or at apex, the veins conspicuous at apex to inconspicuous toward base, entirely glabrous or sparsely to densely covered toward midrib of lower half by light brown to hyaline, prostrate, antrorsely oriented hairs to 1.5 mm long, rarely approaching along midrib to within a few millimeters of apex, the margins glabrous or sparsely to completely lined with hyaline hairs, 0.1–0.5(–0.8) mm long, the auricles usually absent, if present mainly on juvenile leaves (those first produced by twigs), 0.5–4.5 mm long and 0.1–1 mm wide at base, purple, with 2–20 cilia along margins, the oral setae absent or numbering up to 15(–20), most abundant on juvenile leaves, 1–20 mm long on juvenile leaves, 1–10 mm long on higher-order leaves, entirely white or white to stramineous above and stramineous, brown or purple at base, scabrous to glabrous at base, the outer ligule absent or to 0.6 mm long, flaring to prostrate, rarely fringed with short hairs, the inner ligule 0.1–0.5(–1) mm long, densely to sparsely covered with hyaline erect hairs, 0.02–0.2 mm long; *blades* green to dark green; variable in size according to sequence of growth (juvenile leaves with blades usually longer and wider than higher-order leaves), (0.6–)1–3.5(–5) cm wide and (7.8–)9.8–24(–25.6) cm long, narrowly oblong, blades on flowering branches gradually smaller and narrowly ovate toward spikelets, abaxially glabrous to sparsely covered with hyaline hairs



0.2–1.5 mm long, adaxially glabrous to sparsely covered with hyaline hairs (0.1–)0.5–1.5 mm long, one edge with 0–5 rows of prickly-hairs, the margins scabrous, the apex acuminate, base obtuse, narrowing into a pseudopetiole, the pseudopetiole abaxially usually glabrous to sparsely pubescent, adaxially glabrous to densely pubescent, a pulvinus present on each side of pseudopetiole base, rarely absent, stramineous, brown, green, or purple, usually glabrous but sometimes sparsely pubescent. *Synflorescence* borne on leafy or leafless, delicate, branching twigs. *Pseudospikelets* 2–5(–8) per synflorescence or solitary, narrowly ovate, erect to arcuate, elliptic in cross section, disarticulating between the florets. *Main florescence* (1.5–)2.2–9(–10) mm long and 3–8 mm wide; uppermost vegetative internode 0.5–3.6(–9) mm long and 0.5–2 mm wide at apex, sparsely to densely covered on distal half with hyaline hairs 0.1–0.2 mm long, ventral half glabrous to sparsely covered with hyaline hairs to 0.1 mm long; gemmiparous bracts 0–3, stiff, stramineous to light brown, occasionally mixed with light green and/or marked with purple along margins; uppermost gemmiparous bract 7–14 mm long, 4–7 mm wide, ovate, the apex acute with mucro 0.2–1.4 mm long, the margins glabrous, the surface glabrous throughout or sparsely to densely pubescent, the nerves 11–17; empty bracts absent; lowest rachilla segment (1.7–)2.6–7(–8.5) mm long, 1–2.3 mm wide at apex, the surface similar to rachis. *Florets* 3–14(–18), upper 2 or 3 underdeveloped; *lemma* stiff, similar in color to bracts but usually somewhat darker, 10–17 mm long, 6–10 mm wide, ovate, the apex acute with mucro 0.1–1 mm long, the margins glabrous, the surface glabrous or sparsely to rarely densely pubescent, becoming sparse to absent toward edges and apex, the nerves 11–17; *palea* papery, stramineous, occasionally marked with purple on margins of keels, usually with winged keels exerted beyond margins of lemma, 7–14 mm long, 2–3 mm wide between keels, elliptic to obovate, the apex acute, the margins densely ciliate, the surface between keels pubescent on distal  $\frac{2}{3}$  to  $\frac{1}{2}$ , other surfaces glabrous; *lodicules* 3, filmy, transparent and colorless to translucent and entirely stramineous, sometimes orange-red at base, the surface and margins sparsely ciliate, the anterior pair 2–5.2 mm long, 1–2.5 mm wide, ovate to elliptic to obovate with apex acute to obtuse to truncate, rarely acuminate, the posterior one 2–5.2 mm long, 0.8–1.8 mm wide, ovate to elliptic to obovate with apex acute to acuminate; *stamens* 6, filaments hyaline, very delicate, anthers stramineous, rarely marked with purple, 5–8 mm long, the base sag-

ittate, apex rarely minutely penicillate; *ovary* brown, rectangular (in longitudinal section), 0.3–1.5 mm wide, glabrous; *style* yellow, ovate, 1.3–2.5 mm long, 0.3–1.3 mm wide at base, the base truncate, the apex acuminate, the surface densely pubescent; *stigmas* 3, hyaline to light purple, surface pubescence similar to style; *fruit* a dry caryopsis, 5 mm long, sulcate.

*Ecology.* Principally near rivers, streams, and wet places, or other openings in forest canopy in well-drained to wet soils, on flat or sloping terrain, from sea level to 1,800 m; also cultivated in urban areas, on farms, and along roadsides.

#### KEY TO THE SUBSPECIES OF *GUADUA ANGUSTIFOLIA*

- 1a. Culm leaf ligule continuous to one or both margins, occasionally curved up before reaching both margins; foliage leaf sheath glabrous; outer ligule 0–0.3 mm high, not flaring to slightly flaring; abaxial foliage leaf blade usually glabrous; synflorescence borne on leafless to rarely leafy twigs; pseudospikelets erect to rarely slightly arcuate; main florescence (4–)5–7(–8) mm wide ..... subspecies *chacoensis*
- 1b. Culm leaf ligule nearly always curved up before reaching margin, rarely continuous to one or both margins; foliage leaf sheath glabrous to pubescent toward midrib of lower half, rarely along midrib of upper half; outer ligule 0.1–0.9 mm high, slightly flaring to clearly flaring; abaxial foliage leaf blade commonly with scattered hairs, occasionally glabrous; synflorescence borne on leafy or occasionally leafless twigs; pseudospikelets erect and arcuate or entirely erect; main florescence (2–)3–6(–7) mm wide, but if synflorescence contains only erect pseudospikelets, these less than 5 mm wide ..... subspecies *angustifolia*

#### a. *Guadua angustifolia* Kunth subsp. *angustifolia*. Figures 1, 6–10.

- Bambusa guadua* Humb. & Bonpl. *Plantae Aequinotiales* 1: 63, pl. 20. 1806. *Guadua angustifolia* Kunth, *Synopsis Plantarum* 1: 252, 253. 1822. *Nastus guadua* (Humb. & Bonpl.) Sprengel, *Caroli Linnaei . . . Vegetabilium* 2: 113. 1825. TYPE: Nov. Granada [Colombia], *Bonpland* 2003 (lectotype, here designated, P not seen, photo and fragment, US; isoelectotypes, B not seen (and possibly destroyed), fragment, US; possible additional isoelectotype, P).
- Guadua aculeata* Rupr. ex Fourn. *Mexicanas Plantas . . . Pars secunda Gramineae*, p. 130. 1886. *Bambusa aculeata* (Rupr. ex Fourn.) Hitchcock, *Contr. U.S. Natl. Herbarium* 17: 387. 1913 [as *Bambos*]. TYPE: Mexico. Veracruz: Colipa, 1841, *Karwinsky* 944 (lectotype, here designated, LE, fragment, US).
- Guadua inermis* Rupr. ex Fourn. *Mexicanas Plantas . . . Pars secunda Gramineae*, p. 129. 1886. TYPE: Mexico. Veracruz: Papantla, 1841–1842, *Karwinsky* 946b (lectotype, here designated, LE, fragment, US).
- Guadua intermedia* Rupr. ex Fourn. *Mexicanas Plantas*



... Pars secunda Gramineae, p. 130. 1886. TYPE: Mexico. Veracruz: Papantla, *Karwinsky 1464* (holotype, LE, fragment, US).

*Guadua aculeata* Rupr. ex Fourn. var. *liebmanniana* Camus, *Les Bambusées*, p. 112. 1913. TYPE: Mexico. Veracruz: Colipa, Mar. 1841, *Liebmman 136* (lectotype, here designated, US).

*Guadua angustifolia* Kunth var. *bicolor* Londoño, Rev. Acad. Colomb. Cienc. 17: 379. 1989. TYPE: Colombia. Cundinamarca: vía Honda-Guaduas, "Km 119," 930 m, 29 Jan. 1987, *Londoño & Quintero 70* (holotype, COL not seen; isotypes, COL not seen, TULV not seen, US not seen).

*Culms* 7–25 m tall, 7–15 cm diam., exceptional culms to 30 m tall and 20 cm diam. *Culm leaf ligule* almost always curved up before reaching leaf margin, rarely continuous to one or both margins. *Foliage leaf sheath* entirely glabrous to covered toward midrib of lower half, rarely along midrib of upper half, with light brown to hyaline, prostrate, antrorsely oriented macrohairs, 0.05–1.5 mm long, the collar 0.1–0.9 mm long, slightly flaring to clearly flaring, the oral setae 0–13(–20), the auricles absent to present, the ligule 0.1–0.9(–1.2) mm long, pubescent. *Foliage leaf blade* (7.5–)10–20(–23) cm long, 0.9–3.2(–5) cm wide, glabrous to commonly with scattered hyaline hairs. *Synflorescence* borne on leafy or occasionally leafless twigs. *Pseudospikelets* erect to arcuate, 1.5–9(–10) cm long, (2–)3–6(–7) mm wide, containing (4–)5–17(–18) florets.

*Distribution.* Occurring sporadically from Veracruz and Puebla, Mexico, south through Guatemala, Honduras, El Salvador, Nicaragua, and Panama; common in Colombia in middle to upper watersheds of Cauca and Magdalena rivers and east into southern llanos and Amazon basin; common in Ecuador west of Andes and along rivers of Amazon basin; sporadic in northern Amazon basin of Peru; also collected from a few localities in southern Venezuela (possibly cultivated) and Guyana (Figs. 2, 3).

*Common names.* Tarro, Otate (Central America); Guadua, Caña brava, Caña mansa, Garipa (Colombia and Ecuador); Marona, Ipa (Peru); Jua-jua, Puru puru (Venezuela).

*Additional specimens examined.* MEXICO. VERACRUZ: District of Papantla, Tajín, 26 Mar. 1948, *Kelly 180* (US); Colipa, Mar. 1841, *Liebmman 137* (LE, US); San Sebastian, *Liebmman 135* (US); Colipa River valley 3 km W of Vega de Alatorre, *Young 205* (FLAS, US, XAL). PUEBLA: Cuauhtapanaloyán, Cuetzalán, 4 Apr. 1981, *Basurto et al. 409* (MEXU). GUATEMALA. SAN MARCOS: Finca Ona near El Quetzal, *McClure 21562* (US). IZABAL: Boca Ancha, 5 July 1948, *McClure 21675* (US); vicinity of Quiriguá, *Standley 24035* (NY, US); between Virginia and Lago Izabal, Montaña del Mico, *Steyermark 38762*

(F); Quiriguá, *Weatherwax 39* (US). RETALHULEU: N of San Luis, 29 Jan. 1948, *McClure 21572* (US); between Nueva Linda and Champerico, *Standley 87743* (F). SUCHITEPEQUEZ: Hacienda Chicolá along Chicolá River, *McClure 21488* (US); Puente ICAM at 21 km from Chicolá on the road to Quezaltenango via Mazatenango and San Francisco Zapotitlán, 30 Jan. 1948, *McClure 21573* (US); El Pito, experiment gardens of the Instituto Agropecuario Nacional (from Honduras), 13 Feb. 1948, *McClure 21591* (US); near Pueblo Nuevo, *Standley 66933* (F, US). SOLOLA: Finca Monte de Oro, *Popenoe 976* (US). HONDURAS. ATLANTIDA: Tela, Lancetilla Experiment Station, a native species, *McClure 21673* (US); Lancetilla Valley near Tela, *Standley 53166* (F). EL SALVADOR. AHUACHAPAN: road from San Salvador to Ahuachapán, 20 km W of Santa Ana, *McClure 21608* (US); nursery "Las Actuales Circunstancias" near Ahuachapán, 8 Apr. 1948, *McClure 21615* (US). NICARAGUA. ZELAYA: El Recreo, agricultural experiment station, wild along Chiwawa Creek at farthest rice test plot, *McClure 21477* (US). PANAMA. CHIRIQUI: Boquerón, 2 Apr. 1937, *Allen 300* (US). CANAL ZONE: near property shed at the experiment gardens, Summit, 15 May 1945, *McClure 21339* (US). GUYANA. Banks of rivers, Dec. 1892, *Jenman 6370* (US); Aruka River, *Jenman 7274* (US). VENEZUELA. AMAZONAS: Río Casiquiare, base of Piedra Guanare, *Wurdack & Adderley 43186* (P, US, VEN). COLOMBIA. META: Reserva Nacional La Macarena, frente a la desembocadura del Río Sansa, Apr. 1957, *Idrobo 2600* (COL); Puerto López, *Little & Little 8333* (COL); margen izquierda del Río Guayabero, raudal de la Macarena (Angostura #1), *Pinto & Bischler 314* (COL, P, US); municipio de San Martín, vereda Bajo Humadea, margen derecha del Río Humadea, Finca la Isla, *Pinto & Bernal 1675* (COL, P, VEN). CAQUETA: Solano on Río Caquetá, 12 Mar. 1945, *Little & Little 9779* (COL, US). ANTIOQUIA: Granja de Las Mercedes, en Venecia, *Gutiérrez & Barkley 17C609* (COL, US). CUNDINAMARCA: Nocaima, Hacienda Tobia, 15–20 Jan. 1942, *García-Barriga 10685* (COL); La Vega, camino a Nocaima, 27 Jan. 1942, *García-Barriga 10648* (COL, US); La Esperanza a San Javier, camino de herradura y línea del ferrocarril a Girardot, 15 Jan. 1947, *García-Barriga 12202* (COL, US); carretera de Pacho a Talauta, 1 Nov. 1940, *Jaramillo-Mejía 25* (COL); La Esperanza, *Obregon 108* (COL); Tocaima, *Pérez-Arbeláez 2416* (COL); La Mesa, Tena, *Triana s.n.*, Dec. 1854 (US). CALDAS: Chinchiná, *McClure s.n.*, 31 Dec. 1949 (US). RISARALDA: Pereira, en la vereda de Mundo Nuevo, *Rodríguez 001* (COL). QUINDIO: municipio de Pijáo, Hacienda Paraguaycito (FEDECAFE), *Ramírez s.n.*, 4 Nov. 1976 (COL). HUILA: 1 km SW of San Antonio Fortelecillas, 20 km E of Neiva, 25 Jan. 1943, *Fosberg 19831* (US); along Río Neiva, Juntas, near Algeciras, *Little & Little 7805* (COL, US). VALLE: Cordillera Occidental, vertiente occidental, hoyo del Río Anchicaya, El Paso, *Cuatrecasas 14858* (US); cerros cerca de Alcalá, 15 Nov. 1946, *Cuatrecasas 22874* (COL, F, P, S, US); Bitaco, 14 Aug. 1949, *García-Barriga 8005* (COL, US); La Cumbre, *Killip 5998* (US); Hacienda Miranda near Palmira, *McClure 21233* (US); Palmira, wild on campus of the agriculture school, *McClure 21737* (US). CAUCA: near Popayán, *Alston 8566* (COL, US); Popayán, Cauca Valley, *Lehmann 7639* (US); Hacienda García, Corinto, between Miranda and Padilla, *McClure 21232* (US). NARIÑO: Tumaco, right bank of Rosario River, 5 km above Caserío de Santa María, *Romero Castañeda 5197* (COL). ECUADOR. NAPO: Arajuno, flood plain of Arajuno River,



72 mi. NE of Shell-Mera, *McClure* 21360 (US); S shore Aguarico River near Zancudo Lake, *Young* 25 (FLAS, QCA, US); across Napo River from Misahuallí, *Young* 66 (FLAS, QCA, US); 48 km N of Tena on road to Baeza, *Young* 84 (FLAS, QCA, US); 4 km W of Borja on road to Baeza, *Young* 95 (FLAS, QCA, US); 6 km W of Coca Falls on road to El Charco, *Young* 99 (FLAS, QCA, US). CARCHI: environs of Chical, 12 km below Maldonado on Río San Juan, *Madison et al.* 4671 (F, US); River San Juan bridge crossing near Maldonado, *Young* 140 (FLAS, QCA, US). ESMERALDAS: Concepción, up Río Santiago to Selva Alegre, near village of Timbura, *Little* 6390 (F, UC, US); Playa de Oro, *Little* 6409 (F, UC, US); Río Guayabamba, 10 km E of Quinindé, *Little & Dixon* 21251 (F, US); Río Bravo, 0.5 km S of Cayapas River, *Young* 67 (FLAS, QCA, US); junction of San Miguel and Cayapas rivers, *Young* 68 (FLAS, QCA, US). PICHINCHA: between Santo Domingo and Quinindé, *Acosta-Solís* 14013 (US); Nanegalito, N of Tandayapa, *Acosta-Solís* 17157 (US); Quito-Santo Domingo road, *McClure* 21400 (US); outskirts of Santo Domingo, *McClure* 21401 (US); Rancho Ronald, km 28 on Santo Domingo-Chone road, *Young* 117 (FLAS, QCA, US). MANABI: Mount Monte Cristi, near Colorado, SE of Manta, *McClure* 21375 (US); Cerro de Balsamo, *McClure* 21376 (US); Chagualu, 7-8 mi. N of Chone on the Quito road, *McClure* 21377 (US); Cerro Plácido, hillside above San Plácido, *McClure* 21378 (US); San Antonio on Chone River, *McClure* 21380 (US); edge of Porto Viejo, *McClure* 21382 (US); Salima, 3 km SE of Jama, *Young* 65 (QCA, US). TUNGURAHUA: trail up to Hacienda La Gloria from Río Negro bridge on way across the Río Pastaza, *McClure* 21361 (US); between San Francisco and Machay along road in valley of Pastaza River, 13 July 1945, *McClure* 21364 (US); 11 km E of Baños on road to Puyo, *Young* 53 (FLAS, QCA, US). COTOPAXI: Tene fuerte, Río Pilaló, km 52-53, Quevedo-Latacunga, *Dodson & Gentry* 12252 (MO). BOLIVAR: Charquiyacu, descenso inferior externo de la Cordillera Occidental, *Acosta-Solís* 6127 (F). LOS RIOS: Estación Biológica Pedro Franco Dávila at Jauneche on road from Mocachi to Palenque on Estero Peñafiel, *Dodson & Gentry* 12689 (US); Pichilingüe Experiment Station, *Little* 6437 (F, UC, US); Hacienda Camarones, 30 mi. N of Quevedo, *McClure* 21347 (US); near Pichilingüe on Quevedo River flood plain, *McClure* 21354 (US); Hacienda Pichilingüe, *McClure* 21384 (US). GUAYAS: Teresita, 3 km W of Bucay, *Hitchcock* 20415 (US); Panigón Plantation, 8 mi. S of Milagro, *Hitchcock* 20585 (US); Daule on Daule River, *McClure* 21383 (US). MORONA-SANTIAGO: along the path El Descanso near the Yungaza River N of Limón on the Cuenca-Macas road, *Young* 32 (QCA, US); 17 km S of the junction of the Negro and Paute rivers on the Cuenca-Sucúa road, *Young* 33 (QCA, US). ZAMORA-CHINCHIPE: 3 km E of Zumbi towards the Nangaritza River, 1 June 1980, *Young* 151 (FLAS, QCA, US). EL ORO: between El Carmen and El Blanco, 23 Nov.-15 Dec. 1987, *Albert de Escobar* 983 (MO); El Tablón, 6 km E of Portovelo, *Fosberg & Giler* 23013 (US). PERU. LORETO: km 174 from Huánuco on the Tingo María-Pucallpa road, *McClure* 21437 (US). AMAZONAS: confluence of Ickiti and Cenepa, *Berlin* 626 (MO, US).

b. *Guadua angustifolia* Kunth subsp. **chacoensis** (N. Rojas) S. Young & W. Judd, comb. et stat. nov. *Bambusa chacoensis* N. Rojas, Bull. Acad. Int. Geogr. Bot. 26(4): 157.

1918. TYPE: Argentina. Chaco: Depto. Bermejo, General Vedia, riberas del Río de Oro, 23 July 1974, *C. Quarín et al.* 2384 (neotype, here designated, CTES; isoneotypes, F, G, US). Figures 9, 10.

*Culms* 12-20 m tall, 10-15 cm diam. *Culm leaf ligule* continuous to one or both margins or occasionally curved up before reaching margin. *Foliage leaf sheath* glabrous, the collar (0-)0.1-0.2(-0.3) mm long, not flaring to slightly flaring, the oral setae (0-)1-5(-7), the auricles absent, the ligule 0.1-0.3(-0.4) mm long, pubescent. *Foliage leaf blade* (6.5-)9.2-15.6(-25.6) cm long, (0.5-)0.7-1.7(-2.8) cm wide, glabrous or with only a few scattered hairs. *Synflorescence* borne on leafless to rarely leafy twigs. *Pseudospikelets* erect to rarely slightly arcuate. *Main florescence* (2.8-)3.2-5.6(-6) cm long, (4-)5-7(-8) mm wide, containing (5-)6-10(-11) florets.

*Distribution.* Paraguay and Paraná river watersheds of eastern Paraguay, northeastern Argentina, and southeastern Brazil; also possibly along Uruguay River in northeastern Argentina and northwestern Uruguay (Fig. 4).

*Common names.* Tacuara, Tacuaruzú.

*Specimens examined.* BRAZIL. PARANA: just outside of Foz do Iguaçu on the border between Brazil and Paraguay, along the Rio Paraná on the Brazilian side, *Davidse et al.* 11233 (F, NY). ARGENTINA. MISIONES: Depto. San Ignacio, Peñon Reina Victoria, *Krapovickas & Cristóbal* 28759 (US); vicinity of Puerto Aguirre, *Curran* 676 (US); Puerto León, *Curran* 677 (F, US); Eldorado, *Meyer* 5.567 (UC); Iguazú Falls, *Rodriguez* 486 (MO, US). CORRIENTES: Depto. Concepción, Rincón de San Pedro, *Burkart et al.* 30.687 (US); vicinity of Goya, *Curran* 313 (US); Depto. Ituzaingó, Isla Apipé Grande, Puerto San Antonio, *Krapovickas et al.* 23851 (CTES, G, MO, US); Depto. Ituzaingó, Rincón Ombú Chico, *Krapovickas et al.* 25470 (CTES, ENCB, G, MO, US); Depto. Capital, Riachuelo y Ruta 12, borde de bosque de Urunday, *Maruñak* 635 (CTES, US); Isla San Martín, frente a Ituzaingó, *Meyer* 6284 (UC); Depto. Capital, Arroyo Riachuelo y Ruta 12, *Quarín et al.* 1859 (CTES, US); Depto. Concepción, Paso Aguirre, Rincón de San Pedro, *Quarín* 2870 (CTES, US); Depto. Mercedes, 75 km N of Mercedes, Laguna Trin, Culantrillar, *Quarín* 3182 (CTES, US); Depto. Capital, puente Pesoa, Arroyo Riachuelo, *Schinini et al.* 6819 (CTES, US). CHACO: Depto. Bermejo, General Vedia, riberas del Río de Oro, *Quarín et al.* 2384 (CTES, F, G, US); Casa Lata, *Rojas* 11719 (S). PARAGUAY. SAN PEDRO: Colonia Nueva Germania, *Rojas* 2311-10492 (US); Alto Paraguay, Primavera, *Woolston* G112 (UC, US). CAAGUAZU: entre Coronel Oviedo y Colonia Independencia, orillas Arroyo Tebicuary, *Burkart* 18741 (US). CAAZAPA: Salitre Cué, barranca selvática del Río Tebicuary-guazú, *Pavetti & Rojas* 10959a (US). CENTRAL: Ruta 2 y Arroyo Mboiy, *Schinini* 10956 (US). PARAGUARI: forest near Sapucay, *Hassler* 1730 (G); Sapucaí, près de Paraguarí, *Balansa* 4346 (US).



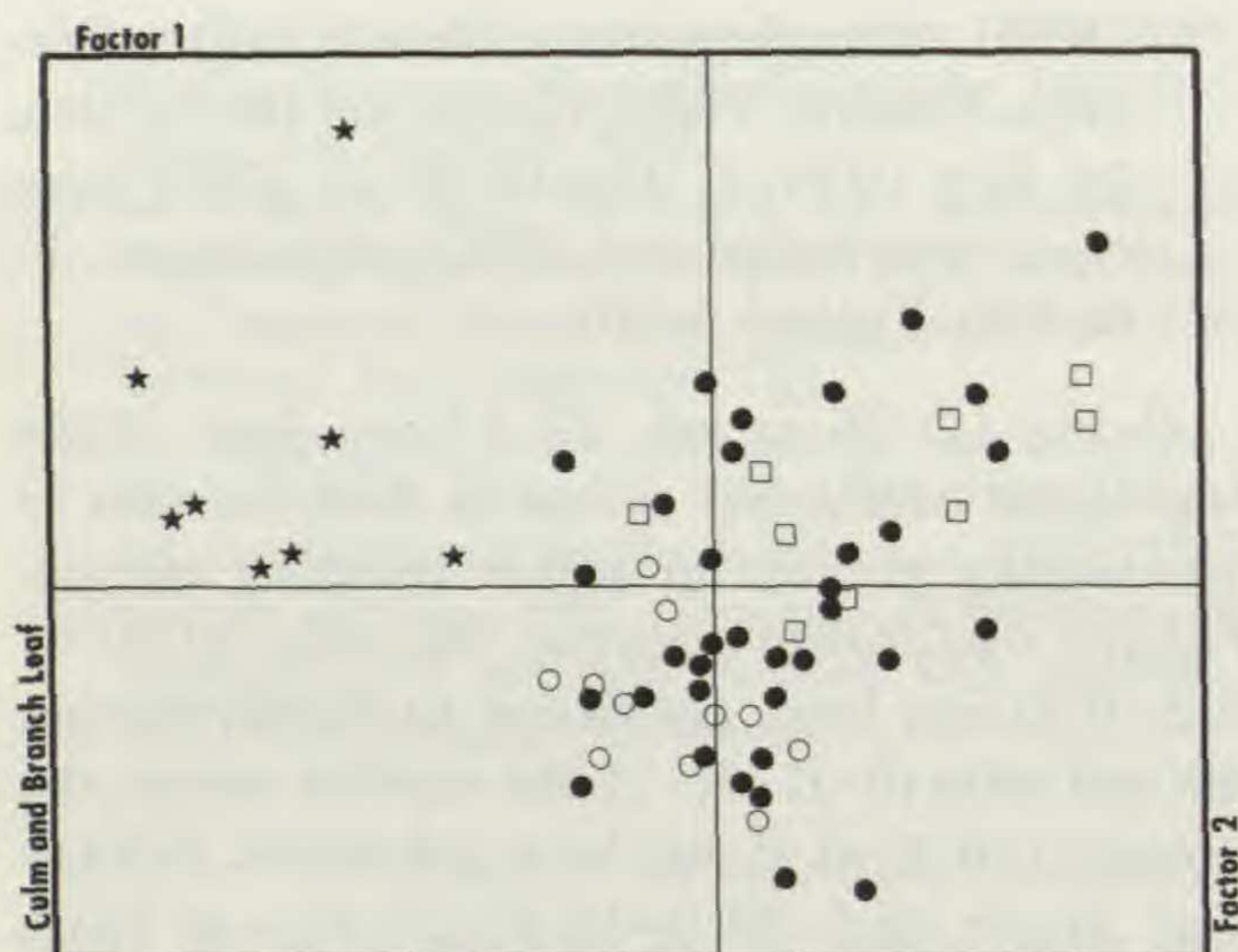


FIGURE 13. Principal components analysis of culm and foliage leaf data; the first two components account for 23.5% of the variation. Stars = subspecies *chacoensis*; dots = subspecies *angustifolia* "western populations"; open circles = subspecies *angustifolia* "northern populations"; squares = subspecies *angustifolia* "eastern populations."

The range of *Guadua angustifolia* is extraordinarily broad in comparison to most bamboos. Most plant and animal species with extensive ranges show some infraspecific variation, but until now there have been no detailed studies of the variation within any of the species in the genus *Guadua*. The geographical barriers between populations of *G. angustifolia* are wide enough to have favored some degree of local divergence. The variation is relatively complex, with vegetative and floral characters showing differing and mosaic patterns of variation. Thus, populations (and taxa) may be separated only by using sets of correlated characters.

The populations that make up *Guadua angustifolia* subsp. *angustifolia* are more similar in both vegetative and floral features to each other than they are to the southern populations here recognized as *G. angustifolia* subsp. *chacoensis*. These populations of *G. angustifolia* subsp. *angustifolia* can be divided into three main groups: the Mexican and Central American populations (i.e., "northern race," formerly called *G. aculeata*); the western Colombian and western Ecuadorian populations (i.e., "western race") including the few specimens from Venezuela (possibly introduced) and Guyana; and the Amazon basin populations (i.e., "eastern race") from Colombia, Ecuador, and Peru.

Vegetatively, these three population groups or "incipient geographical races" are very similar. Principal components analysis of culm and branch leaves shows the variation of the eastern and northern populations to be contained wholly within that of the western populations (Fig. 13). A similar

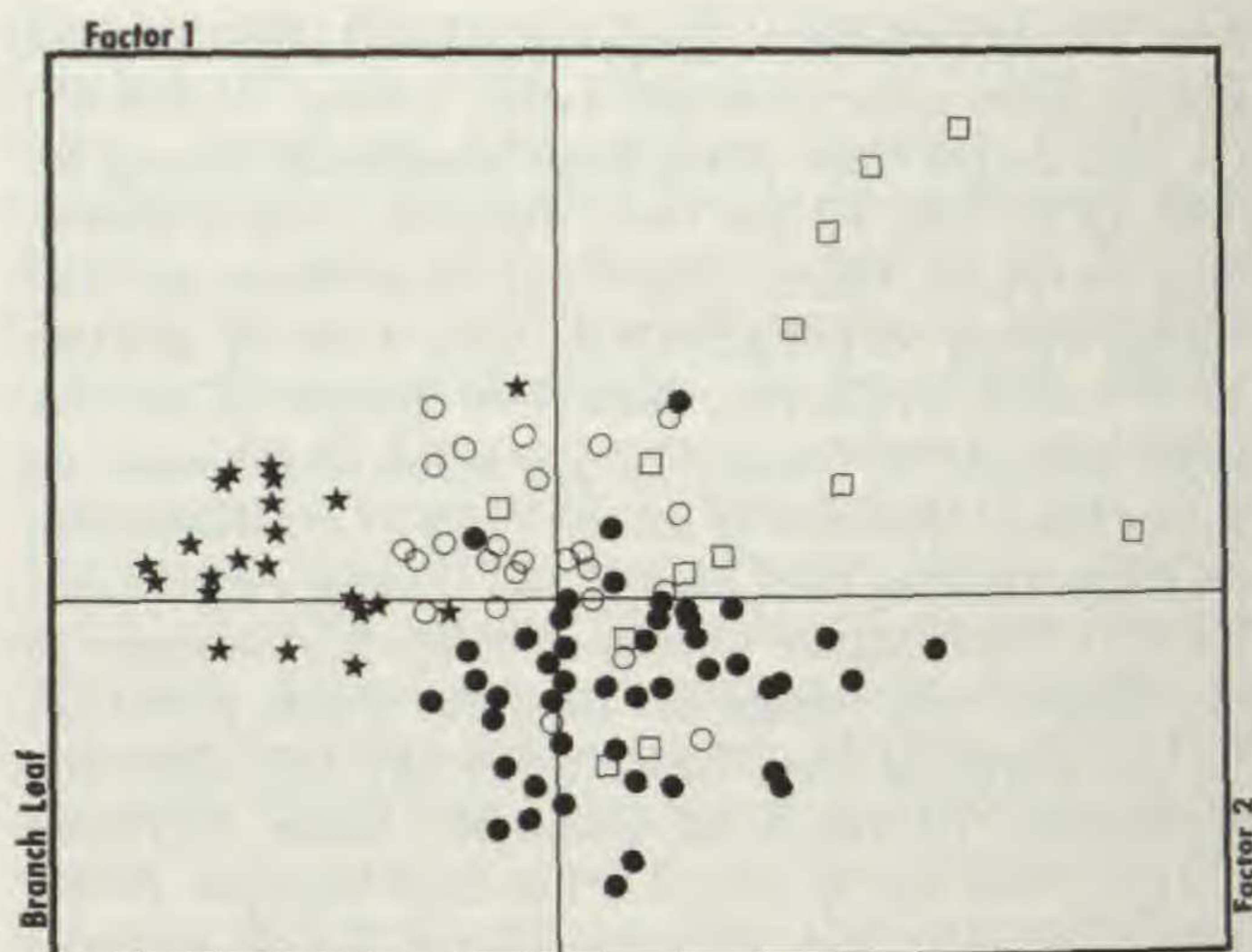


FIGURE 14. Principal components analysis of foliage leaf data; the first two components account for 25.1% of the variation. Stars = subspecies *chacoensis*; dots = subspecies *angustifolia* "western populations"; open circles = subspecies *angustifolia* "northern populations"; squares = subspecies *angustifolia* "eastern populations."

overlapping pattern of variation in these populations is seen when only branch leaves are considered (Fig. 14). The northern populations tend to have foliage leaf sheaths that are glabrous, whereas the sheaths of the eastern and western populations usually possess macrohairs. In the eastern populations some specimens possess distinct auricles on the foliage leaves and tend to have longer ligules and larger pulvini, especially on the juvenile leaves (Fig. 10b). These characteristics do not appear anywhere else within the range of the species, and their influence is evident on the PCA diagram based upon branch leaf characters (Fig. 14). Some of the specimens (i.e., those with auricles) are placed well away from the "central cluster," but other eastern specimens (those lacking auricles) are not separated. This character does not seem to be constant within the eastern populations, and its taxonomic value is in doubt. We conclude here that these eastern populations do not warrant formal taxonomic recognition. The first author noted the general trend toward smaller culms in the Oriente of Ecuador (Young, 1981), but no systematic study of culm size has been carried out, due to the lack of adequate collections.

Inflorescence characteristics are also variable among these three "incipient geographic races" of *Guadua angustifolia* subsp. *angustifolia*, but no large gaps are present. The "western race" possesses the largest spikelets, i.e., (3.1-)3.5-9(-10) cm long, which have a tendency to arch. The "northern race" seems to show a cline in spikelet length, with the spikelets becoming shorter from Panama northward. They are (1.5-)2-5.3(-7) cm long and erect or rarely slightly arching (Fig. 17b,



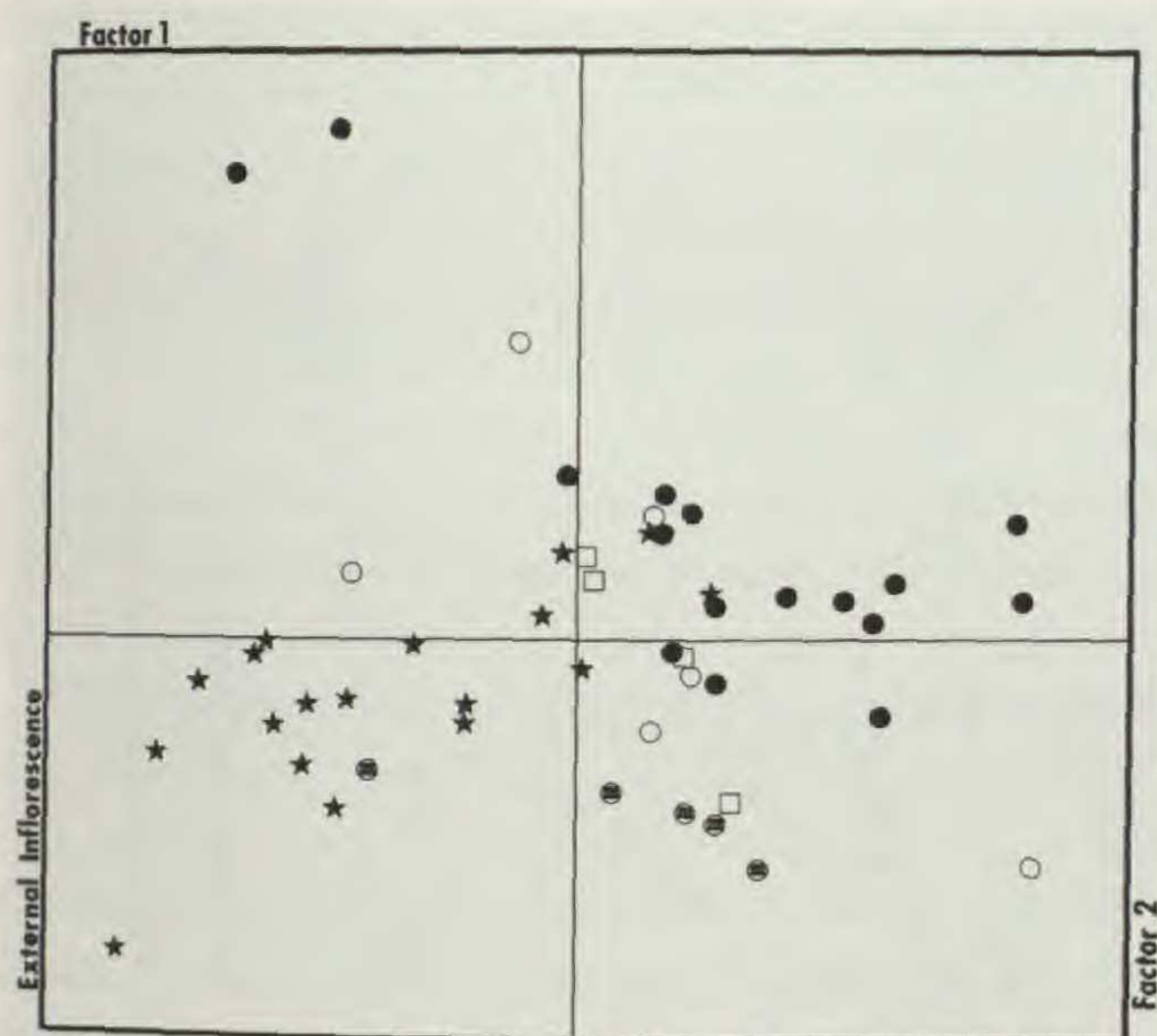


FIGURE 15. Principal components analysis of external inflorescence data set; the first two components account for 27.8% of the variation. Stars = subspecies *chacoensis*; dots = subspecies *angustifolia* "western populations"; open circles = subspecies *guadua* "northern populations" from Central America; circles with letter "m" = subspecies *angustifolia* "northern populations" from Mexico; squares = subspecies *angustifolia* "eastern populations."

d). Principal components analysis of external inflorescence characters shows the Mexican specimens to be most different from the western populations, with other Central American plants bridging the "gap" between these areas (Fig. 15). When the PCA of data from dissected spikelets is examined (Fig. 16), an analysis involving a greater number of characters (and showing the influence of internal structures such as palea and style length and style hairs on the principal component loadings), there is a small gap between these "races" of subspecies *angustifolia*. The "northern race" tends to have longer styles and style hairs than either the "eastern race" or "western race," and their paleas are slightly longer. This analysis should be interpreted with caution, however, since the sample size is very small. In McClure's (1955) detailed descriptions of *B. guadua* and *B. aculeata* in the *Flora of Guatemala*, there are only four significant differences between the two, and they all involve floral characters. These include gemiparous bract length, spikelet length, floret number per spikelet, spikelet cross section, and anther connective extension. The present study shows more overlap in these same characters when more specimens are taken into account than were available to McClure (see descriptions).

The "eastern race" also tends to have short pseudospikelets that are not arched (Fig. 17c), but some plants from this region have pseudospikelets comparable to those of western plants. For ex-

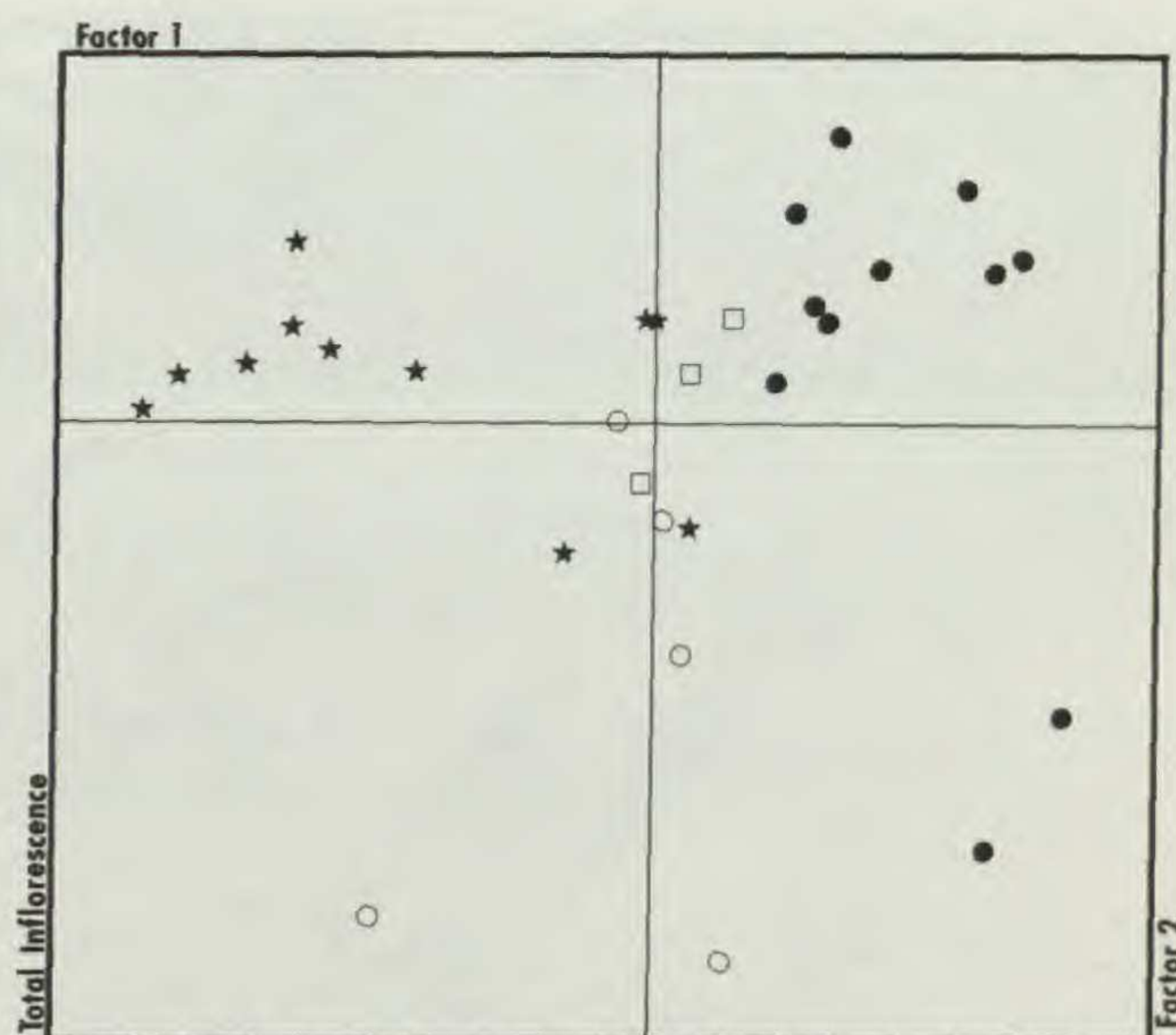


FIGURE 16. Principal components analysis of total inflorescence data set; the first two components account for 31.2% of the variation. Stars = subspecies *chacoensis*; dots = subspecies *angustifolia* "western populations"; open circles = subspecies *angustifolia* "northern populations"; squares = subspecies *angustifolia* "eastern populations."

ample, Figure 17a depicts the pseudospikelets from a clump growing in the southern Amazonian region of Ecuador. They are longer and more arched than is typical for plants in the eastern region and are comparable to many from the "western race" of subspecies *angustifolia*. This illustrates the need for more material from this region before any formal taxonomic decision concerning the status of these "incipient geographical races" can be made.

In contrast to the situation involving the "incipient geographic races" within *Guadua angustifolia* subsp. *angustifolia*, *G. angustifolia* subsp. *chacoensis* shows a number of vegetative and floral characters that allow these southern populations to be consistently distinguished from any other populations of the species. The degree of vegetative difference is shown in PCA of both branch and culm and branch leaf characters (Figs. 13, 14) where there is a clear, although not large, gap between *G. angustifolia* subsp. *chacoensis* and the remaining populations of *G. angustifolia*.

In subspecies *chacoensis* the ligule of the culm leaf is often continuous to the leaf margin (Fig. 9d). In other respects it is similar to the culm leaf of subspecies *angustifolia*. The foliage leaves are the most distinctive vegetative feature of this subspecies. The sheaths are always glabrous. The collar is shorter and less flared, the ligule possesses longer hairs, and the pulvini are smaller than those of subspecies *angustifolia*. The blades are almost always glabrous abaxially and rarely possess any macrohairs adaxially. Subspecies *angustifolia* of-





FIGURE 17. Spikelet variation in *Guadua angustifolia* subsp. *angustifolia*. — a. Long spikelets of "eastern race"; Young 151. — b. Long spikelets of "northern race"; McClure 21573. — c. Short spikelets of "eastern race"; McClure 21364. — d. Short spikelets of "northern race"; Karwinski 944.



ten has macrohairs on one or both surfaces except on primary leaves. Blade widths also tend to be narrower in subspecies *chacoensis*, but there is a fair amount of overlap in this character.

Culm characteristics of the two subspecies were not compared because of the lack of material of subspecies *chacoensis*. From label data and photos the culms do not appear to be significantly different, although subspecies *chacoensis* does not attain the height of some culms of subspecies *angustifolia*.

Some degree of separation is also shown in PCA of floral characters. *Guadua angustifolia* subsp. *chacoensis* tends to have shorter and more erect pseudospikelets than the western populations of *Guadua angustifolia* subsp. *angustifolia*, and therefore shows some overlap with the eastern northern populations in PCA based upon these characters (Figs. 15, 16). However, subspecies *chacoensis* almost always has wider pseudospikelets than the eastern and northern populations of subspecies *angustifolia*, and therefore is easily distinguished (see key). It shows more of an overlap in pseudospikelet width with the western populations of subspecies *angustifolia*. The synflorescences of subspecies *chacoensis* are almost always borne on leafless twigs, whereas those of subspecies *angustifolia* often are intermixed with leafy twigs or have leaves on the same twigs. However, there are some specimens of subspecies *angustifolia* that have pseudospikelets borne only on leafless twigs. The color of pseudospikelets is difficult to determine because of developmental changes, but those of subspecies *chacoensis* tend to be brownish (vs. more or less stramineous in subsp. *angustifolia*). Again, this difference is not absolutely consistent, but is only a general trend. Paleas tend to be longer and wider in subspecies *chacoensis*. The lengths of the style and style hairs are longer in subspecies *chacoensis* than in the western and eastern "races" of subspecies *angustifolia*, but are similar to the "northern race."

The flowering cycle for *Guadua angustifolia* has not been accurately determined, but it appears to be close to 30 or 35 years. In 1976, extensive flowering was observed in clumps of subspecies *angustifolia* in Colombia and subspecies *chacoensis* in Argentina. This may provide evidence that the two taxa are conspecific. In addition, the overall similarity of the two subspecies (especially when compared to other sympatric species of the genus *Guadua*) indicates that they are best treated as one polymorphic species.

In past descriptions of *Guadua angustifolia* from Colombia and Ecuador (McClure, 1955, 1966; Hidalgo, 1978; Maecha Vega & Echeverri Res-

trepo, 1983), various growth forms have been described. Local people who work with "guadua" on a daily basis distinguish among three forms known as "guadua macana" or "caña brava," "guadua cebolla" or "caña mansa," and "guadua rayada." *Guadua rayada* is recognized as variety *bicolor* by Londoño (1989). *Guadua macana* is distinguished from *guadua cebolla* by having a smaller diameter, more basal branches that are thorny and hinder entrance to the clump, and stronger wood with more resistance to decay. *Guadua macana* is used for all kinds of heavy construction, whereas *guadua cebolla* is usually split longitudinally and used as bamboo boards called "esterilla" in Colombia and "picada" in Ecuador. *Guadua rayada* possesses vertical yellow or white stripes between the nodes and is stronger than *guadua cebolla* but not as strong as *guadua macana*. Londoño & Prieto (1983) described *guadua macana* as by far the most common form in the Cauca Valley of Colombia, with the other forms being found scattered within clumps of *macana*. These forms are not separated geographically or ecologically and are probably due to slight genetic differences or even environmental and/or competitive effects. However, further study is needed (e.g., breeding studies, common garden experiments) in order to clarify their status.

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A REVISION OF *PANICUM*  
SUBGENUS *PHANOPYRUM*  
SECTION *LAXA* (POACEAE:  
PANICOIDEAE: PANICEAE)<sup>1</sup>

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ABSTRACT

*Panicum* subg. *Phanopyrum* sect. *Laxa* is revised. Twelve American and one Asian species are treated in this work, in which exomorphological and anatomical characters are considered. Section *Laxa* is defined mainly as perennial plants of humid places, with membranous ligules, spikelets unilaterally disposed on the inflorescences, upper antheria membranous to indurate, with silica bodies and simple papillae, a basic chromosome number of  $x = 10$ , and conspicuous fusoid cells in the leaves. Possible relationships of *Laxa* to other sections of subgenus *Phanopyrum* and subgenus *Steinchisma*, as well as with other genera of the Paniceae such as *Homolepis* and *Hymenachne*, are discussed. A key to the species as well as an anatomical description of the section and photomicrographs of six species, morphological descriptions of the species, and distribution maps are presented. The taxonomic position of *Panicum scabridum* and *Panicum grande* are also discussed.

The group *Laxa* was informally established within *Panicum* by Hitchcock & Chase (1910); these authors initially included seven species in the group: *Panicum polygonatum* Schrader, *P. longum* A. Hitchc. & Chase, *P. pilosum* Sw., *P. laxum* Sw., *P. cupreum* A. Hitchc. & Chase, *P. hians* Elliott, and *P. exiguiiflorum* Griseb. In 1915, Hitchcock & Chase validly published the group, adding to *Laxa* *P. stevensianum* A. Hitchc. & Chase and *P. milleflorum* A. Hitchc. & Chase, defining the group mainly by the inflorescence type, with spikelets unilaterally disposed on short pedicels. Hitchcock & Chase (1915) also described *P. stagnatile* and *P. grande*, not grouping these species within *Panicum*.

Pilger (1931) raised the *Laxa* group to sectional level and in 1940 characterized the section by the inflorescence type, considering approximately 20 species as belonging to the section. Examples are *P. grumosum* Nees, *P. pernambucense* (Sprengel) Mez ex Pilger, and *P. gynerioides* (Griseb.) Pilger (= *P. prionitis* Nees).

Hsu (1965) differentiated *Laxa* as having 3-nerved lodicules, membranous ligules, papillose upper antherium, and a basic chromosome number of  $x = 10$ . Hsu noted relationships between *Laxa* and sections *Tenera* and *Verrucosa* and stated that *Laxa* should be excluded from subgenus *Panicum*

and included in subgenus *Megathyrsus*, because of the ornamentation of the upper antherium.

The classification of *Panicum* has undergone many changes in recent years, due mainly to the study of the Kranz syndrome (Brown, 1977). These new anatomical and physiological characters showed that section *Laxa* sensu lato included species differing markedly in exomorphological and photosynthetic characteristics. Brown & Brown (1975) cited *P. milioides* Nees ex Trin. (= *P. hians*) as a species with physiological characters intermediate between Kranz and non-Kranz species, as is the case in other species such as *P. spathellosum* Doell and *P. decipiens* Nees ex Trin. (Ku et al., 1976; Ku & Edwards, 1978; Morgan & Brown, 1979; Morgan et al., 1980). Brown (1977) placed these three species in a separate genus *Steinchisma* Raf., with intermediate  $C_3/C_4$  photosynthesis, spikelets not unilaterally disposed on the inflorescences, upper antherium entirely papillose, and lower palea expanded at spikelet maturity. Brown (1977) included eight species of the *Laxa* group within subgenus *Sarmentosum*, whereas he placed others in the *Grandia* group. The *Grandia* group in the sense of Brown is a complex of Kranz species, i.e., *P. petersonii* A. Hitchc. & E. Ekman and *P. prionitis*, and non-Kranz species, such as *P. grumosum*, *P. pernambucense*, and *P. stagnatile*.

<sup>1</sup> The first author acknowledges support of a fellowship from the John Simon Guggenheim Memorial Foundation, to which he expresses appreciation. Zuloaga's fieldwork in Colombia and Venezuela was carried out under a grant from the National Geographic Society, to whom he is also grateful.

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Zuloaga (1987) defined section *Laxa* by the inflorescence type, nervation of the spikelet, and upper anthecia ornamentation. He included approximately 15 species in the section, which he placed in the non-Kranz subgenus *Phanopyrum* of *Panicum*. *Panicum prionitis* and *P. petersonii* were excluded and placed in section *Prionitia* of subgenus *Agrostoides*, and *P. grande* was ungrouped within subgenus *Phanopyrum*. *Steinchisma* was considered as a separate subgenus of *Panicum*.

In the present treatment, section *Laxa* is defined and diagnosed by its exomorphological and anatomical characters. In addition, the systematic position of *P. scabridum* Doell, *P. condensatum* Bertol., *P. auritum* J. S. Presl ex Nees, and *P. grande* is discussed in relation to this definition of section *Laxa*.

#### MATERIALS AND METHODS

Procedures of classical taxonomy were used in this study. Specimens were examined from the following herbaria: B, BAA, BAF, BLA, CEN, CEPEC, COL, F, G, GH, HB, IAN, IBGE, K, LE, LIL, M, MO, MY, NY, P, PORT, R, RB, SI, SP, UB, US, VEN, W. Field methods included collection and drying of specimens for herbaria, preserving leaves, spikelets, and other structures in FAA (formalin-ethanol-acetic acid) and transferring them to 70% ethanol in the laboratory.

Laboratory studies were made using a Wild M5 dissecting microscope. For the scanning electron microscope (SEM), anthecia were removed from herbarium specimens, secured on stubs, carbon coated in a vacuum evaporator, and coated with a gold-palladium alloy. These specimens were then viewed in a Cambridge S4-10 or Cambridge Stereoscan 259 Mk2 scanning electron microscope operating at 10–20 kV.

Transverse sections of leaf blade material, 10  $\mu$ m thick, were sectioned after desilicification in 30% hydrofluoric acid, dehydration in a methyl cellosolve series and infiltration and embedding in Tissue Prep (Fisher Scientific). The sections were stained in safranin and fast green. For abaxial epidermis scrapes, the mesophyll and vascular tissue was removed with a scalpel and camel's hair paintbrush. These were stained in safranin.

The standardized terminology of Ellis (1976, 1979) was used for the anatomical descriptions. The following abbreviations are used: vb/s—vascular bundles; 1'vb/s—first order vascular bundle/s; 3'vb/s—third order vascular bundle/s; ibs—

inner bundle sheath; mestome sheath; obs—outer bundle sheath; parenchyma sheath.

Freshly fixed material of the following taxa was studied: *Panicum grumosum* (3 accessions), *P. hylaeicum* (4 accessions), *P. laxum* (13 accessions), *P. pernambucense* (6 accessions), *P. pilosum* (9 accessions), *P. polygonatum* (7 accessions), and the sectional anatomical description is based on this material. This sample was augmented by herbarium material of *P. auritum* (2 accessions), *P. bresolinii* (1 accession), *P. condensatum* (2 accessions), *P. leptachne* (2 accessions), *P. stagnatile* (2 accessions), *P. stevensianum* (6 accessions), *P. grande* (3 accessions), *P. scabridum* (6 accessions) and *P. longum* (1 accession), but anatomical detail was difficult to ascertain in much of this material.

Vouchers for this study are marked with an asterisk (\*) in the specimens examined section of the taxonomic treatment.

#### EXOMORPHOLOGICAL CHARACTERS

Species of section *Laxa* grow in humid places, either along the borders of woods or forming dense colonies on the banks of streams and rivers. Examples are *Panicum pernambucense*, *P. grumosum*, and *P. stagnatile*. *Panicum laxum* and *P. pilosum*, on the other hand, are pioneer species and usually invade modified habitats.

The plants are short-rhizomatous or stoloniferous, decumbent and rooting and branching at the lower nodes, with hollow internodes and leaf blades flat, linear to ovate-lanceolate. The ligules are membranous, shortly laciniate or occasionally ciliate at the apex, commonly absent in *P. pilosum*.

#### INFLORESCENCE

The inflorescence type is one of the most distinguishing characters of this section, the spikelets being arranged unilaterally on first- or second-order racemose branches. All included species possess this feature.

First-order branches are alternate, subopposite, or whorled toward the base, diverging in all directions in relation to the main axis. A small membranous bract is usually present at the first node of the panicle. This bract has pilose margins or sometimes is reduced to a small arc of papillose hairs.

There is a gradient in the degree of ramification of the inflorescence. Paired spikelets are present on the ventral side of first-order branches in species such as *P. pilosum*, *P. leptachne* Doell, *P. condensatum*, and *P. longum*. In the other species